

**EVALUATION OF RESTRICTED-AREA CULLING STRATEGIES TO CONTROL
LOCAL RED FOX DENSITY**

by

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Zoology)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

April 2015

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Abstract

Lethal control of red foxes is often implemented on restricted areas where immigration from neighbouring sources is expected to make it difficult to keep local fox density low. The justification of lethal wildlife control should include demonstrating its effectiveness. To this end, population dynamics modelling may help to assess the performance of different control strategies in a range of real-world circumstances. A Bayesian state-space model for within-year fox population dynamics was developed that could be fitted to data on daily culling effort and success obtained from gamekeepers on shooting estates in Britain. The estimation model included parameters for key population processes within the culling area: immigration, cub recruitment and non-culling mortality. A simulation-estimation study showed that given a minimum of three years' data the estimation of fox density and demographic parameters was reliable. Informative priors for the key model parameters were constructed using empirical data and meta-analysis. Data from 22 estates were modelled on a two-weekly time-step. Most estates achieved some suppression of the fox population relative to estimated carrying capacity, but few maintained consistently low densities. The number of foxes killed was a poor indicator of culling effectiveness, highlighting the need for modelling. Estimated immigration rates onto estates were typically high, indicating rapid replacement of culled foxes. There was unexpectedly high spatial variation among estates in estimated carrying capacity and immigration rate. There was evidence from a limited subset of estates that the variable density of released game birds may explain this. The food requirement of the fox population during the nesting period was assumed to indicate predation pressure on wild birds. Alternative culling strategies to reduce this requirement were evaluated using posterior parameter estimates from some estates. Culling concentrated

in spring and summer only was more effective than culling uniformly throughout the year. Autumn-only culling was not an effective strategy for wild birds. Open-loop strategies were most effective as culling effort was used all the time. However, closed-loop strategies, where culling effort was conditional on feedback from simulated field-sign searches, achieved similar effects on food requirements using less effort. This revealed trade-offs between effectiveness, cost and animal welfare.

Preface

This dissertation is original, unpublished work of myself, T.A. Porteus. Several datasets were used in the analyses for which I was not involved in the survey design or data collection:

- Data used in Chapter 2 and Chapter 7 resulted from the Fox Monitoring Scheme, a survey conceived by J.C. Reynolds and resourced by the Game & Wildlife Conservation Trust (GWCT). All data entry and analysis was performed by myself.
- Data used in Chapter 4 and Chapter 7 were obtained from the National Gamebag Census, a long-term annual dataset administered by GWCT.
- Data used in Chapter 6 resulted from a distance sampling study conceived by J.C. Reynolds and M.J. Heydon, and resourced by GWCT. Data were collected by J.C. Reynolds, M.J. Heydon and M.J. Short. Data entry was performed by M.J. Heydon and M.J. Short. All analysis was performed by myself.
- Data used in Chapter 8 resulted from a study on snare use conceived by J.C. Reynolds and M.J. Short, and resourced by GWCT. Data entry was performed by J.C. Reynolds and M.J. Short. All analysis was performed by myself.

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Acknowledgements

I could not have completed this research without the help, encouragement and support of many people. I would sincerely like to thank my supervisor, Dr. Murdoch McAllister, for providing me with the opportunity to study at UBC. He introduced me to Bayesian statistics and his expertise and enthusiasm for research were invaluable to me in developing this thesis. I would like to express my gratitude to Dr. Jonathan Reynolds (Game & Wildlife Conservation Trust), whose patience and mentorship has enabled me to reach this stage in my career. I would also like to thank the other members of my committee, Dr. Carl Walters (UBC Fisheries Centre), Dr. Steve Martell (International Pacific Halibut Commission) and Dr. Villy Christensen (UBC Fisheries Centre), for providing valuable insights into population dynamics modelling and for feedback on my thesis.

Funding and data for this thesis were provided by the Game & Wildlife Conservation Trust (GWCT). I must thank them for their continued financial support and I look forward to my future work there. I thank many GWCT staff for their assistance, but specifically I would like to acknowledge Mike Short for sharing his understanding of practical fox control issues and for reminding me about the joys of fieldwork.

I have been fortunate to have a talented group of fellow Zoology graduate students to learn from during my time at UBC, many of who have become good friends. I specifically thank Shannon Obradovich for keeping my computer in the Fisheries Centre running while I was in the UK so I could finish my simulations. I also need to thank the unconditional support of a fantastic group of friends (the “Gong Show”) away from my department who have kept me sane by making me laugh with their exploits. Most importantly, thank you to my mum for emotional and financial support, and to my brother Ed for moral support and inspiring me to keep a balance between work and exercise.

Finally, I owe my deepest thanks to my wife, Cosima. She has been a constant source of love and laughs and without her patient support and encouragement, especially through difficult times, I could not have been able to do this. Thank you for sharing your life and the doctoral experience with me.

In memory of my Dad, who sparked my interest in wildlife biology and sadly passed away
before the end of my doctoral journey.

Chapter 1: General introduction

1.1 Management of wildlife populations

Populations of wildlife species are managed for three main reasons: 1) conservation, which aims to maintain and, where appropriate, increase populations of threatened species; 2) harvesting, which aims to maintain populations of exploited species at productive levels; and 3) population control, which attempts to decrease populations of pest species below some critical level (Shea *et al.* 1998). Management of wildlife populations can achieve these aims by controlling the human activities affecting them (Hilborn 2007). Management of a population requires the development of strategies prescribing actions that strike a suitable balance between effectiveness, efficiency and humaneness (Reynolds & Tapper 1996). Each alternative strategy will differ with respect to these considerations, leading to a decision-making problem as managers must choose between alternative strategies that may prescribe very different actions (Dorazio & Johnson 2003). The ability to make effective strategic decisions depends upon having suitable information on the state of the population under management. The task for wildlife managers is to understand their local situation and balance the trade-offs to determine the most efficient and humane strategy that is likely to achieve the best balance between conflicting objectives.

Conservation, harvesting, and population control are often interrelated. In both game management for harvesting and in species conservation, control of predator populations has long been recognised as one of the key management actions available to managers (Leopold 1933). Control of predator and pest species for goals of game management and threatened species conservation is a widespread practice and there is plentiful evidence of the positive effect predator removal can have on prey populations (Côté & Sutherland 1997; Holt *et al.* 2008; Salo *et al.* 2010). Nevertheless, the net benefit of predator control is increasingly subject to public scrutiny, and scientific evaluation of the potential effectiveness and ecological outcomes of culling is required (Fall & Jackson 2002). Definition of measurable management objectives is therefore a fundamental step in determining management strategy – otherwise performance of the strategy cannot be evaluated.

It has been recommended that success of population control strategy should be measured not in terms of predator density, but by a change in prey density or prey breeding success (Sinclair, Fryxell & Caughley 2006). However, in many situations – particularly at local scales – evaluating objectives relating to prey density is not straightforward. There may not be any data on prey populations, or it may be difficult to monitor them accurately. The relationship between predator density and prey density may not be well defined, as demonstrating the size of the effect of removing predators typically requires detailed study (Hone 1994), e.g. eight years for predator removal (Tapper, Potts & Brockless 1996; Fletcher *et al.* 2010) or predator exclosure studies (Krebs *et al.* 1995). The detection of effects must also be at the relevant scale. There may not be any observable response in the prey population to culling effort due to compensatory mortality caused by other predator species (Salo *et al.* 2010), due to overwhelming stochastic events, or perhaps most importantly, because the predator control was ineffectually implemented. In the event of small or absent responses to control by prey populations, managers judging their strategy solely in terms of prey-related metrics are thus left with a dilemma. Their options for future action include stopping culling and directing effort elsewhere (e.g. habitat management); continuing as before in the belief that the control effort was having an effect; or adopting an alternative predator control strategy in the belief that the previous strategy wasn't working. Measuring the performance of a strategy directly in relation to predator density could reduce these decision-making problems.

Wildlife research (e.g. a predator removal study) is designed to generate data and infer ecosystem relationships using models that describe the system, with statistical tests determining the significance of hypotheses about the unknown parameters of these relationships (Prato 2005). The conventional approach managers have used to make strategic decisions is to take generalisations (rules-of-thumb) from such quantitative research together with previous personal or collective experiences and combine these into a strategy. For example, if a study found that culling during the spring using a particular method was the most effective, a manager might adopt this strategy in their local situation, particularly if they have previous successful experience at this time of year. Actions are typically not designed to be responsive to changing field conditions. While this is a practical and pragmatic

approach to developing a management strategy, the location and scale of the research will often have been very different to the situation where the strategy is to be applied. Consequently, management actions within the strategy may not be appropriately targeted to the new situation, where the dynamics of the controlled population may be different. This can result in management that is ineffective in both the short- and long-term and which comes with excessive economic and welfare cost, leading to greater risk of mismanagement and conflicts of interest among different stakeholders. Effective management can be reliably achieved only by tailoring strategy closely to the objectives for each local situation.

1.2 Red fox control in Britain

The red fox *Vulpes vulpes* is commonly managed as a pest throughout its range (Macdonald & Reynolds 2004). Foxes are widely distributed throughout the Northern hemisphere and Australia, having been introduced to the eastern USA and Australia for sport hunting in the 1800s (Baker & Harris 2008). Given this wide distribution, many alternative strategies and methods to control fox populations have been used. In Britain, foxes are frequently brought into conflict with game and conservation interests as they are predators of both game (e.g. pheasant *Phasianus colchicus*, redleg partridge *Alectoris rufa*, grey partridge *Perdix perdix*; Reynolds & Tapper 1995a, 1996; Tapper, Potts & Brockless 1996; Draycott *et al.* 2008) and other threatened species (e.g. brown hare *Lepus europaeus*, lapwing *Vanellus vanellus*, stone curlew *Burhinus oedipnemus*; Reynolds & Tapper 1995b; Fletcher *et al.* 2010). The generalist nature of foxes as predators means they have the potential to drive prey species into declines via depensatory predation, particularly when fox abundance is enhanced by human practices that enhance one or more of the prey species (Reynolds & Tapper 1996; Sinclair *et al.* 1998). Foxes can cause problems to livestock farming through predation of lambs, poultry and piglets, though the economic scale of these losses is debated (Heydon & Reynolds 2000a; Moberly *et al.* 2003). Foxes are also vectors for pathogens and parasites, e.g. the mite *Sarcoptes scabiei* which causes scabies in humans and sarcoptic mange in canids; and (though not currently in Britain) rabies and the tapeworm *Echinococcus multilocularis* which can cause human alveolar echinococcosis (Craig 2003; Soulsbury *et al.* 2007).

Britain has a long history of predator control, and regional efforts to reduce fox numbers for the benefit of animal husbandry have taken place at least since Saxon times (Reynolds & Tapper 1996). Foxes are native to Britain, but their ecological status is heavily altered by the historical activities of man. These include changes in habitat following agricultural intensification; elimination of natural predators (e.g. wolf *Canis lupus* and lynx *Lynx lynx*); introduction of new prey species (e.g. rabbit *Oryctolagus cuniculus* and pheasant); and the provision of other new food resources in urban areas (Tapper 1999). These changes have generally been advantageous to the fox, generating conflicts with human interests and new ecological relationships with other species. Predator control to benefit small game species in Britain began in the early nineteenth century on restricted areas of land privately managed for game hunting (Tapper 1992). At this time, intensive control by gamekeepers led to regional extinction of some mammalian predator species, though the fox was afforded some protection due to its status as sporting quarry for fox hunts (Reynolds & Tapper 1996). Following the Second World War, social change and agricultural intensification resulted in a fall in the numbers of gamekeepers in full-time employment (Tapper 1992). The consequent release from culling pressure resulted in the fox population increasing through the second half of the twentieth century (Tapper 1992; Whitlock, Aebischer & Reynolds 2003).

The paradigm that common generalist predators including the fox can limit the numbers of some wild prey species while being supported by a much broader resource base underlies the use of predator control in game management and threatened species conservation in Britain. It is evidenced in Britain by formal predator removal experiments, well-documented case examples, and quantitative studies, but remains a much debated topic (Reynolds & Tapper 1996; Tapper, Potts & Brockless 1996; Stoate & Leake 2002; Fletcher *et al.* 2010; Reynolds *et al.* 2010b; Ewald, Potts & Aebischer 2012; Potts 2012; White *et al.* 2014). Nevertheless, it is not the purpose of this thesis to question the motives for culling foxes, but rather to study the process itself and the extent to which it is successful in controlling fox density.

The rural British landscape is a patchwork of relatively small landholdings such as farms, shooting estates, and nature reserves. Most landholdings are smaller than 10 km², but some large estates may be several times this size. Most predator management occurs locally within these restricted areas by gamekeepers, but a large proportion of landholdings (57%) are not under any form of fox control (Defra 2012). This proportion does vary by region, reflecting general differences in management aims (Heydon & Reynolds 2000a). There is little co-ordinated large-scale regional fox control due to excessive cost; but where this is achieved by collaboration between many neighbouring gamekeepers it can result in suppressed regional fox density (e.g. East Anglia, Heydon & Reynolds 2000a; b). Fox control is particularly associated with shooting estates with the aim of benefitting gamebird populations for harvesting (Tapper 1992; Reynolds & Tapper 1996; Heydon & Reynolds 2000a). The other main aims of fox control are elimination or reduction of losses to fox predation of livestock or threatened wildlife species (Reynolds 2000).

Methods of culling foxes in Britain have changed over time with changes in legislation and advances in technology. The current legal methods are 1) shooting with a rifle or shotgun, 2) restraint in non-locking neck snares, and 3) live-capture cage traps. Foxes may also be flushed from underground by terriers to be shot above ground. Foxes captured alive must be dispatched humanely with a firearm. Each method has potential welfare costs and these must be balanced with effectiveness and efficiency. There is no statutory closed season so foxes of any age and sex may be killed (Heydon & Reynolds 2000a). Outlawed methods include leg-hold traps, self-locking neck snares, poison and fumigants (Reynolds & Tapper 1996). The Hunting Act 2004 (www.hmsso.gov.uk) recently outlawed hunting with scent hounds and the use of terrier dogs to kill cubs at breeding earths. Though there is a regional difference in prevalence of culling method used (Heydon & Reynolds 2000a), the majority of culling is done by night shooting using a rifle and spotlight, a method known as lamping.

There are many decisions a gamekeeper must make when determining a fox control strategy. These are related to the objectives of control which on a shooting estate will be to improve the harvest of game. Shooting estates can be broadly split into two extreme types:

wild bird estates and released bird estates. Wild bird estates aim to achieve a harvestable surplus from wild stocks, while released bird estates hand-rear birds in pens and release them into the wild prior to the start of the shooting season (Tapper 1999). There are many questions that gamekeepers must decide upon, including:

- When in the year should culling effort be used?
- How intensive does the culling effort need to be?
- Is there a threshold when culling can be stopped?
- When does continuing to cull become inefficient?
- Which culling method is best, and does this change with the time of year?
- Are there non-target capture or animal welfare costs with the choice of method?
- What monitoring data should be collected to learn from and improve the culling program?

For each decision to be made there will be a set of possible management actions, a set of uncertain events associated with each action, and a set of outcomes that must be measured (Ellison 1996).

There are potentially a number of performance measures for fox control on shooting estates: 1) annual harvest (i.e. the gamebag), which can be monitored relatively easily from bag returns; 2) breeding productivity of gamebirds, which requires both spring and autumn counts; 3) survival of released gamebirds, which requires some level of tagging effort; and 4) return rate of released gamebirds (i.e. the proportion of released gamebirds that are shot during the shooting season). But fox control is just one aspect of the management on an estate. Foxes are not the only managed predator species in Britain, with corvids, e.g. carrion crow *Corvus corone* and magpie *Pica pica*, and mustelids, e.g. stoat *Mustela erminea* and weasel *Mustela nivalis*, often being controlled concurrently (Tapper, Potts & Brockless 1996). Habitat management is also an action that can affect game species, and is often applied for this reason, especially to compensate the effects of agricultural intensification. It is therefore very difficult to ascribe a change in these performance measures to fox control alone. In any case, few estates regularly conduct spring and/or autumn game counts, and

even fewer estates monitor the survival of released or wild birds, so there are usually limited data. In absence of data on prey responses which can be attributed to fox control, the gamekeeper can judge the effect of culling only through some measure of local fox population density itself.

Monitoring within-year changes in local fox density is a major challenge. There are a range of methods available for monitoring predator populations (Gese 2001; Wilson & Delahay 2001; Long *et al.* 2008). However, established field methods to estimate fox density, e.g., using mark-recapture methods, require a level of effort typically unavailable to gamekeepers and are inappropriate in the fast-changing context of intensive culling. Nevertheless, gamekeepers do have local and time-specific information available to them. Field signs and sightings can be used as indices of abundance, as can catch-per-unit-effort. One method, the use of a spotlight and rifle, has much in common with scientific survey methods, and by recording the number of hours of effort and the number of foxes sighted and/or shot it generates data indicative of relative local abundance. Mathematical models can make use of such culling data to produce a quantitative understanding of local fox population dynamics during the culling process, and thereby evaluate its effectiveness. Exploratory models can also be used as “What if...” tools to predict the likely impact of different culling actions (Buckland *et al.* 2007) and identify ways to increase effectiveness.

1.3 Approaches to modelling

In complex ecological systems, predictions from models on the effect of management decisions on populations are subject to several uncertainties including: 1) process uncertainty, resulting from demographic stochasticity and environmental variability; 2) observation uncertainty, resulting from errors in measurement and sampling of ecological systems; 3) structural uncertainty, resulting from incomplete knowledge about how the system should be modelled; 4) parameter uncertainty, resulting from lack of knowledge about the parameter values within a model structure; and 5) implementation uncertainty, resulting from the incomplete control of management actions (Ellison 1996; Williams 1996; Parkes *et al.* 2006).

Formerly, the approach to strategic decision making relied heavily on frequentist statistical methods (Wade 2000; Prato 2005). A fundamental aspect of frequentist statistics is that inference is based on the expected frequency that the observed data are likely to be obtained with hypothetical replicates of sampling (McCarthy 2007). The assumption that a study is representative of the system and can be repeated independently is usually violated in most ecological studies due to process uncertainty making each study unique (Ellison 1996; Prato 2005). Frequentist methods such as sensitivity analysis or bootstrapping can be used to evaluate the effect of parameter uncertainty on decision outcomes, and have previously been used to evaluate fox management strategies at the landscape scale in Britain (Rushton *et al.* 2006). However, these methods can fail to reveal the effects of uncertainty and are difficult to interpret (McAllister & Kirkwood 1998). Relationships between population density and relative abundance indices are also often non-linear (Parma *et al.* 1998) and may only be known for a certain population density and under a limited set of habitat and environmental variables. This makes it unsafe to generalise to individual locations with other circumstances. Frequentist methods are further limited by independent treatment of the results of different experiments or studies, which does not allow synthesis of those results (Ellison 2004; Prato 2005).

Bayesian statistical methods offer an alternative approach to dealing with the uncertainty inherent in ecosystem management, with Bayesian inference differing from frequentist inference in several epistemic ways. Bayesian probability allows ranking of the credibility of different hypotheses (e.g., about a given parameter value or model structure) in light of the sample data. In contrast, frequentist inference provides probabilities for the data arising given a particular hypothesis (such as a null hypothesis). The definition of probability is thus different, with the frequentist approach allowing only probability statements about observed data. In contrast, the Bayesian approach allows probability to be defined as an individual's degree of belief in the likelihood of an unobservable event or hypothesis, and as such can be used to make probabilistic predictions about the state of the system. The Bayes posterior probability distribution therefore allows for a formal incorporation of uncertainty in management models (Walters & Ludwig 1994), and management questions are able to be answered directly as the result is a probability statement

about the credibility of different hypotheses given the data obtained. This stands in contrast to frequentist probability statements, such as the commonly used P -value that relates to the expected long-run frequency distribution of potential results as extreme or more extreme than the set of results obtained if the null hypothesis happened to be correct (Reckhow 1990). This makes it easier for managers to communicate predictions about strategic decisions to decision-makers and stakeholders.

The principal advantage of Bayesian inference is that it explicitly incorporates prior knowledge in the form of a prior probability distribution (Ellison 1996, 2004; Wade 2000; Prato 2005; McCarthy 2007). The prior is used along with sample data to compute the posterior on which inference is performed. Allowing inference to take an iterative progression means that as new data are collected the model interpretation is updated and improved. Informative priors can reduce uncertainty and improve estimation performance by constraining the model within reasonable biological limits. The concerns with use of informative priors in Bayesian models are their subjectivity and potential to overwhelm posterior estimates if they are too informative relative to the data (Dennis 1996). Provided care is taken to ensure that prior information is used in a logical and sensible manner, these concerns must be weighed against the advantage of making inferences about populations on which data are scarce (Martin *et al.* 2013). The value of using suitable informative priors has been shown whether they are derived from expert knowledge (Martin *et al.* 2005; Kuhnert, Martin & Griffiths 2010), published data (McCarthy & Masters 2005; Martin *et al.* 2013), or other analytical methods (McAllister, Pikitch & Babcock 2001; McAllister, Stanley & Starr 2010). Bayesian methods are hence well suited to the sparse and noisy data typically available to wildlife managers and uncertainty from biologically important but unknown parameters can be rigorously incorporated into models describing the system (Wade 2000).

Many ecological models are complex, with inference being made on multiple parameters describing different populations. Bayesian hierarchical modelling is a tool for probabilistically sharing information among populations to improve parameter estimates and their precision (Gelman *et al.* 2004; Clark 2005; Cressie *et al.* 2009). The approach uses data from numerous populations, assuming that some hierarchical or nested structure relates them.

This may either be spatial, e.g. within a region (Su, Peterman & Haeseker 2004), or temporal, e.g. within a year (McAllister *et al.* 2004). Parameter estimates for populations that are closer to one another in either space or time may also be assumed to be more similar than for populations that are further away. For these situations it is possible to extend the hierarchical approach to explicitly incorporate the spatial or temporal correlation structure into the model, e.g. using a spatially correlated prior distribution (Su, Peterman & Haeseker 2004). Bayesian hierarchical modelling is thus a powerful approach for complex problems where data are sparse and noisy (Clark 2005). The application of Bayesian inference to ecological questions has grown significantly in the past two decades (McCarthy 2007; Gimenez *et al.* 2009; King *et al.* 2010; Kéry 2010). Despite being widely applied in ecology and fisheries science (McAllister *et al.* 1994; Walters & Ludwig 1994; Punt & Hilborn 1997), Bayesian methods have only recently been applied to the management of vertebrate pest species (Chee & Wintle 2010).

1.4 Evaluating management strategies

The adaptive management approach seeks to learn how to manage an ecosystem under uncertainty about the effects of alternative management strategy decisions (Walters 1986). The concepts of adaptive management were proposed in the context of harvesting for fish (Walters & Hilborn 1976; Smith & Walters 1981; Parma & Deriso 1990) and were developed for waterfowl (Williams & Johnson 1995; Williams, Johnson & Wilkins 1996; Johnson *et al.* 1997). More recently the approach has been applied to vertebrate pest control (Parkes *et al.* 2006). The approach proceeds by managing according to a plan in which decisions are made and modified as a function of what is known and learned about the system, including information about the effect of previous management actions (Walters 1986; Parma *et al.* 1998). The first step is to define explicit management objectives and identify performance indicators. Next is to develop alternative management strategies and identify management actions that can be implemented under each strategy to achieve the objectives. Following implementation, the effectiveness of management is evaluated by examining the monitoring data. The management actions are then modified iteratively to

improve management outcomes. In this way, adaptive management involves an iterative Bayesian learning process (Walters 1986; Ellison 1996).

However, despite the intuitive approach to managing real-world problems there are very few examples where it has been applied in its entirety. Among the reasons for this are a failure to embrace uncertainty and difficulties in funding (Walters 2007; Keith *et al.* 2011). The management strategies that are most likely to be informative about a system are also those that are the most risky, and large-scale monitoring effort required to evaluate them is expensive. Such reasons can be understandable under real-world constraints. For example, for a gamekeeper to apply an adaptive management approach would not only require an estate large enough that two or more strategies could be applied concurrently, but also one where economic and conservation costs to wild game populations could be tolerated under a strategy that potentially required a drastic reduction in fox control effort. Few estates have budgets large enough handle these risks and the loss of harvestable game to shoot may result in unemployment for the gamekeeper.

Management strategy evaluation (MSE) is a stochastic computer simulation-based approach to testing a number of alternative management strategies using quantifiable performance measures derived from the operational objectives (Milner-Gulland 2011). It may be used to design adaptive and non-adaptive robust strategies, depending on how the learning process is represented. MSE makes identification and modelling of uncertainties central to the approach, allowing the robustness of alternative management strategies in meeting objectives to be examined. Originally developed as an approach to whale harvest and fisheries management (Kirkwood 1997; Butterworth & Punt 1999; Sainsbury, Punt & Smith 2000), MSE has recently been proposed as a useful approach to solving terrestrial conservation and pest control issues where real-world experimentation is not feasible (Chee & Wintle 2010; Milner-Gulland *et al.* 2010; Bunnefeld, Hoshino & Milner-Gulland 2011). This makes MSE a useful approach in the evaluation of fox control strategies.

MSE makes use of an operating model to simulate the true state of the population dynamics, parameterised using knowledge of the biological processes of the species being managed. To account for process uncertainty the model parameters are usually in the form

of probability distributions, e.g. posterior distributions from Bayesian analyses. It is possible to use a variety of operating models to account for structural uncertainties. Monitoring of the population can then be simulated using an observation model that generates an abundance measure, typically under some simulated observation error and bias to account for observation uncertainty. The observation data are then passed through one of two alternative options to determine a control rule that is either model-based or model-free (McAllister *et al.* 1999). In the model-free approach the control rule is based directly on observed data, while the model-based approach incorporates an assessment model that is used to estimate model parameters and the subsequent control rule is based on the output. Management actions are rarely implemented perfectly, with error coming from two sources: 1) managers not complying with the rules, and 2) individual dynamics of managers (e.g. when and where control occurs; Bunnefeld, Hoshino & Milner-Gulland 2011). An implementation model can account for this uncertainty by simulating the application of the control decisions on the system and the output is the number of animals removed from the population during that time step, which is passed to the operating model as the final phase in the iterative process.

1.5 Aims of the project and thesis structure

The problems faced by managers of fox populations in Britain are shared by all pest and predator control operations attempting to improve the effectiveness of control strategies on restricted areas. These problems relate to the difficulty in understanding the population and how it responds to control effort, namely:

- What effects have past control efforts had on the fox population dynamics within a given area?
- What is the most effective time to use fox control effort to reduce the potential impacts of predation?
- Are all control methods similarly effective at reducing fox density?
- What are the trade-offs between effective and efficient control?

This thesis will attempt to answer these questions using Bayesian modelling methods. The main goals of this thesis are to 1) develop a local-scale population dynamics model that can

be used to estimate within-year fox density on restricted areas such as shooting estates from data which can be collected by gamekeepers, 2) use meta-analysis and empirical data to construct informative prior probability distributions for key model parameters to reduce parameter uncertainty, 3) apply these priors within the developed model to estimate demographic parameters and within-year fox density on a number of estates across Britain; and 4) evaluate the ability of different strategies to meet management objectives on these estates. The thesis is organised into seven data analysis chapters and a summary:

- Chapter 2 presents a description of the data sources that are available on British fox populations and summarises the results from a dataset on the daily culling effort and success of gamekeepers culling foxes on restricted areas.
- Chapter 3 introduces a Bayesian state-space model for within-year population dynamics that incorporates the key population processes at the local scale and which can be fitted to data obtained from gamekeepers. The reliability of the estimations from the model is evaluated using simulation-estimation analysis.
- Chapter 4 presents a methodology for estimating the rate of immigration into culled fox populations and uses a meta-analysis with data from different landscapes to construct an informative prior.
- Chapter 5 uses meta-analysis to construct informative priors for non-culling mortality rate based upon life history invariant and allometric relationships with mortality rate. The effect of senescence in the fox population on the estimated non-culling mortality rate is examined.
- Chapter 6 provides a description of the detection process of foxes by gamekeepers using the lamping culling method. This applies the predation mechanics theory behind Holling's disc equation (Holling 1959a) to define the model parameter which scales the number of foxes sighted to the fox density as the rate of successful search. Distance sampling analysis of fox sighting data and expert judgement is then used to construct an informative prior for the rate of successful search of foxes by gamekeepers.
- Chapter 7 explores the application of the model developed in Chapter 3 to estimate the model parameters and fox density on a number of shooting estates in Britain. The

reconstruction of fox density allows the effect of previous culling efforts to be determined. Local variation in parameter estimates is also examined in relation to data on the density of released gamebirds from a subset of the modelled estates.

- Chapter 8 presents a management strategy evaluation to evaluate alternative fox control strategies that aimed to reduce the food requirement of the fox population during the bird nesting period. This is performed on a subset of the modelled estates which represented the range of ecological conditions experienced on these shooting estates. The control strategies considered differed with respect to the timing of control, e.g. seasonal or year-round, and the culling methods used, e.g. lamping, snaring or removal of cubs at earths.
- Chapter 9 provides a synopsis of the main findings and future avenues of research.

Chapter 2: The British red fox population and the Fox Monitoring Scheme

2.1 Introduction

Control of red foxes (*Vulpes vulpes*) in Britain has different aims, from gamekeepers attempting to ensure a harvestable surplus of either wild or reared game on a sporting estate, to farmers attempting to reduce their livestock losses, and to wildlife reserve wardens attempting to conserve threatened species. Those who attempt to control fox numbers must – consciously or otherwise – adopt a culling strategy that they feel will achieve their aims at their operating scale. For gamekeepers, this is typically a restricted area of $<10 \text{ km}^2$. Strategic decisions include when to time the cull, how long to carry on for, and what method(s) to use. The long tradition of fox management in Britain has led to gamekeepers having their own preferred strategies for controlling foxes, based upon accumulated experiences of which method(s) suits their local situation, and at what particular time of year (e.g. Frain 2006). While this is undeniably useful knowledge, making a poor decision can have consequences, in terms of effectiveness in achieving the aim of control, economic costs to the estate, and welfare costs to the foxes.

The use of population dynamics modelling and management strategy evaluation could potentially help gamekeepers fine-tune their decisions based upon quantitative data on local fox populations. However, inference using models will only ever be as good as the data being used to estimate model parameters – the garbage in-garbage out principle – which makes the use of suitable local scale data critically important. While there is a great deal of published information about British fox populations (Harris *et al.* 1995; Reynolds 2000; Macdonald & Reynolds 2004; Baker & Harris 2008; Aebischer, Davey & Kingdon 2011), much of this is based upon data collected at spatial and temporal scales that are not necessarily appropriate for modelling populations on restricted areas in which culling is performed throughout the year. Estimation of fox density must be on shorter-than-annual time-steps to allow decisions on seasonal control strategy to be made, requiring data on these time-scales. Data specific to individual estates are necessary to obtain parameter estimates representative of the conditions on those estates. This chapter briefly outlines the existing

data on British fox populations and summarises the results of a large survey on local scale fox control effort across Britain that attempted to fill a gap in the available knowledge of how culling effort varies both spatially and temporally.

2.2 The British fox population: numbers and trends

2.2.1 Numbers

Few estimates of absolute density are available because foxes, like many carnivores, are difficult to census directly due to their cryptic behaviour (Reynolds 2000; Gese 2001). Most of the published estimates are from intensive local studies, e.g. using telemetry, earth (den) counts. However, to provide estimates most of these still make assumptions about fox demography, i.e. the numbers of non-breeding females and itinerant foxes, which vary locally, as well as territory size (Reynolds & Tapper 1995a). Density at this scale is highly variable, ranging from 0.025 foxes km⁻² in upland Scotland to over 30 foxes km⁻² in some urban areas where food is superabundant (Macdonald & Reynolds 2004). Extensive regional (>1000 km²) surveys, e.g. using distance sampling, show that density is also variable at this scale, with pre-breeding density estimated to be 0.16 foxes km⁻² in East Anglia, 0.41 foxes km⁻² in mid-Wales and 1.17 foxes km⁻² in the East Midlands (Heydon, Reynolds & Short 2000). Such surveys are expensive, and it is often more practical to estimate relative density (e.g. using indirect methods such as faecal counts, culling records), particularly over larger areas (Sadler *et al.* 2004). Combination of pre-breeding faecal density counts with a measurement of defecation rates in captive foxes enabled absolute density estimation in arable, pastoral, marginal upland and upland landscapes, which was 0.79-2.23, 1.39-1.88, 0.82 and 0.21 foxes km⁻² respectively (Webbon, Baker & Harris 2004). This distribution of densities broadly matches the annual fox bag density (foxes killed km⁻² yr⁻¹) on shooting estates in different regions (Tapper 1992).

National fox population estimates have previously been made by extrapolating from local studies based upon land classification, and suggested a pre-breeding population of 252,000 (95% CI, 204 000-300 000 in 1981 (Macdonald, Bunce & Bacon 1981) and 240,000 (95% CI not reported but authors gave a low reliability rating) in 1995, with annual cub

production of 425,000 (Harris *et al.* 1995). However, the lack of demographic data on foxes in rural habitats made both these population estimates highly uncertain (Harris *et al.* 1995). Density estimates from faecal density counts were combined with the land area in each rural landscape type to give a pre-breeding population estimate of 225,000 (95% CI, 179,000-271,000; Webbon, Baker & Harris 2004), in addition to 33,000 foxes in urban areas (Harris *et al.* 1995).

2.2.2 Trends

Fox population trends over time can be examined using relative abundance indices, especially when these come from long-term surveys. There are around half-a-dozen survey schemes that regularly collect data on foxes as part of multi-species monitoring programmes in Britain. The methods of these various schemes are detailed in the Tracking Mammals Partnership Report (Battersby 2005), and they include the National Gamebag Census (NGC), the Breeding Bird Survey (BBS), the Waterways Breeding Bird Survey (WBBS), Winter Mammal Monitoring scheme (WMM), Mammals on Roads survey (MOR), and the urban-specific Living with Mammals (LWM) and Garden Bird Watch (GBW) surveys. Data from most of these schemes are suitable only for describing national or regional scale yearly relative abundance trends as they do not contain sufficient spatial or temporal resolution to examine trends at local scales over shorter time periods. The data from these survey schemes indicate that there has been a long-term upward trend in the fox population since WWII that stabilised during the mid-1990s, a period during which there has been a concurrent expansion of range into areas from where foxes were historically absent or scarce. There are numerous factors that might explain this increasing trend, but a key one is likely to be the decrease in number of gamekeepers during the twentieth century that resulted in less culling pressure on foxes than in the early 1900s (Tapper 1992). The stabilisation of the trend seen at the end of this period may be the result of a sarcoptic mange epidemic in the mid-late 1990s that heavily affected urban foxes and rural foxes to a lesser extent (Soulsbury *et al.* 2007). Some of these survey schemes provide coarse indices of abundance but suggest that fox populations may show quite large between year variation and regional differences that can change over time (Battersby 2005).

2.2.3 National Gamebag Census

Foxes have been managed on sporting estates across Britain for many centuries (Reynolds & Tapper 1996), meaning there was huge potential for long-term information to be gathered on local fox populations from gamekeepers' records. Established in 1961 by the Game & Wildlife Conservation Trust (GWCT), the NGC is the longest-running survey scheme and was established to provide a central repository of records from participating estates across Britain. The data comprise the numbers of game and predator species killed annually on an estate, known as 'bag data' (Tapper 1992). Sample size of the NGC is large compared to other survey schemes: between 1961 and 2000 the total number of estates contributing data on fox bags to the NGC was 1,051, with an annual mean of 264 ± 18.8 estates (1 s.e., $n=40$). The geographical coverage is also wide due to a substantial proportion of rural GB being managed for game shooting (Tapper 1992). NGC estates cover 5% of the UK by area, though this varies regionally from 15% in eastern Scotland to under 1% in the Midlands (Whitlock, Aebischer & Reynolds 2003). Relative abundance trend analysis using a generalised additive model showed that in the period 1975 to 2000 fox bags increased significantly in south-east England, East Anglia, east and west Midlands, north-east England and east and west Scotland; though no significant change was detected in south-west England, Wales or north-west England (Whitlock, Aebischer & Reynolds 2003). Since 2000, the population has seen an increase in England and Wales, but not in Scotland (Aebischer, Davey & Kingdon 2011).

The utility of the NGC data in fox population dynamics modelling is low, despite the local scale at which data are recorded. The temporal resolution of the data (total annual culls) precludes modelling within-year changes in density, which would be necessary in order to provide advice to managers on seasonal strategy. A further issue is that bag records do not usually contain data on culling effort. A change in bag size may therefore be due to variations in intensity of effort or the control method used over time, rather than changes in fox density *per se*. Observed trends in bag data can be misleading if effort is not taken into account (McDonald & Harris 1999; Reynolds 2000; Sadler *et al.* 2004). In some regions the number of foxes killed is also a poor predictor of fox density because of variable

immigration of juveniles from neighbouring areas (Reynolds 1994), which means the number culled is dependent upon both effort and the regional pattern of productivity and availability of dispersing juveniles (Sadler *et al.* 2004). The trends in the NGC are however supported by relative abundance indices from other survey schemes (Battersby 2005), and given that there are also problems with the landscape-based approach to estimating density, particularly in converting faecal counts to fox density, there is no definite way of knowing which population trend is correct without knowledge on culling effort.

2.3 Fox Monitoring Scheme

In the early 1990s, it was recognised by the GWCT that there was a need to understand how NGC fox bags arose and how the cull on each estate might influence (or not) the within-estate fox population dynamics (J. C. Reynolds, pers. comm.). No suitable data on rural fox populations at the spatial and temporal scale necessary to undertake such an analysis existed at that time, but the value of obtaining data from farmers, gamekeepers, pest controllers and other individuals or groups that were involved in fox control was understood through previous experience (e.g. from the NGC). In addition to the data such managers typically provided to the NGC, i.e. the number of foxes killed and estate size, they could potentially record the date, effort and method used to cull foxes on their estate or farm, the sex, age class and productivity of any foxes culled on a given date, and other information from field signs and direct sightings about fox presence during the year, e.g. the number of active breeding earths. The Fox Monitoring Scheme (FMS) aimed to gather a more informative dataset than was available through the NGC by collecting some of this more detailed data from managers. In later chapters this thesis will use the FMS dataset to model within-year fox population dynamics on individual estates, but to provide suitable background to the dataset the rest of this chapter provides a brief summary of the dataset by detailing how data were collected and providing an analysis and discussion of some general results.

2.3.1 Survey methods

Legislation and Local conditions across Great Britain constrain the choice of fox control methods available to managers in rural estates, and regardless of regional traditions each manager will have a personal preference for particular methods and a range of abilities in implementing them. Fox density differs across Britain (Heydon, Reynolds & Short 2000; Webbon, Baker & Harris 2004), which likely reflects the history and intensity of control in different regions as culling is the chief cause of mortality in rural foxes (Heydon & Reynolds 2000a; b). Together with differing regional management practices this leads to large regional differences in the number of foxes killed per unit area, as shown in results from the NGC (Tapper 1992). Some form of regional representation would be desirable in a survey of fox control effort to illustrate the range of different fox control practices in different regions.

There is no statutory requirement to keep or submit records of fox control efforts, so any survey would be restricted to volunteers who were both willing to record and submit honest details of their fox control effort and success over a long period of time, and permitted to do so by the respective landowners of the estate(s) on which they managed foxes. Potential contributors to the FMS were solicited from an advertisement in a quarterly GWCT membership publication, making the survey self-selecting, and therefore non-random. This limited how regionally representative it could be, with the number of willing volunteers reflecting the prevalence of shooting estates in different regions. For this reason, additional contributors from regions not represented were identified from existing contacts within the GWCT who were likely to be willing volunteers. This gave some representation in each of the regions classified by the NGC, which divides Britain into ten approximately similar sized regions built up using administrative county boundaries (Tapper 1992). Previous experience in handling voluntary survey data from the NGC showed that contributions from individual estates were likely to change over time as both gamekeepers and estate owners changed. As this was likely to be a problem in the FMS, additional contributors were found if others dropped out in an attempt to keep the number of 'active' contributors relatively constant. In total, 122 gamekeepers and professional pest controllers from across Britain registered an

interest in participating in the survey, of which 74 became active contributors to the FMS during the survey.

Each participating contributor was provided with record books in the form of a daily diaries running from 1 January 1996 to 31 August 2000 in which to record quantitative data about their fox control efforts on an estate in. Record books covered either a 'spring-summer' season (April-August) during which cubs recruit into the fox population, or an 'autumn-winter' season (September-March) during which, in absence of immigration, fox numbers can only decrease. This meant 10 different record books were supplied to each contributor to cover this time period, with individual record books returned to GWCT once the period covered was finished. By gathering data on a day-by-day basis, it was hoped the risk of any contributor being able to convincingly falsify data would be small, but to help ensure data reliability all contributors were interviewed by telephone at approximately 6-month intervals during the scheme, i.e. following the return of the most recent record book, at which time any unusual data from previously submitted books were queried. 17 contributors controlled foxes on more than one estate, resulting in the return of 106 separate sets of record books.

It was necessary to cleanse the data as some record book sets were incomplete regarding certain key information necessary for modelling local fox population dynamics. 17 record book sets, mostly from pest controllers, returned data relating to fox control on separate estates within a much larger geographical area without information on the area over which the control effort was applied on a daily basis. These data were considered unsuitable as they could not be used to reconstruct fox density within a restricted-area. These record books were removed from the dataset. 19 record book sets contained less than one full calendar year of data and were also removed as knowledge on seasonal differences in effort was important. Only 11 record book sets were completed for the entire 1996-2000 period, with an average of 48 books (range 40-54) being completed during any one season as contributors came and left the scheme. Out of the 106 record book sets contributed from different estates, 75 remained following the cleansing process from 54 different contributors.

For each day of a completed FMS record book, the data were: 1) the start and finish time of any lamping session completed; 2) the number of foxes seen and number killed by lamping; 3) the number of occupied breeding earths located and the number of adult foxes and cubs killed at them; 4) the number of foxes killed by a) snaring, b) vermin drives, c) using a sit-and-wait method from a high-seat, d) deer stalking, e) using live-capture traps, or f) any other method. These data fields were all unambiguous. Contributors were additionally asked to categorise foxes killed as either 1) adult or juvenile (sub-adult) males, 2) adult or juvenile females, 3) adult or juvenile of unknown sex (for foxes killed but not recovered), or 4) cubs of either sex not yet independent of the breeding earth. By the end of the summer cubs become undistinguishable from adult foxes and so contributors were not asked to judge the age of juvenile or adult foxes killed away from breeding earths. Contributors were asked to submit either recovered carcasses or jaw bones for autopsy by the GWCT. This would enable accurate aging of foxes by tooth sectioning, and if carcasses were recovered, provide a measure of reproductive performance (estimated litter size) by examining uteri for evidence of postpartum placental scars. All autopsy and tooth sectioning procedures were conducted by GWCT research staff, while data entry, cleaning and analysis was performed by the author.

2.3.2 Results from the FMS dataset

2.3.2.1 Type and location of contributors and estates

The 54 contributors to the FMS were predominantly gamekeepers working full-time (59%) or part-time (30%). The remaining 11% of contributors were either professional fox controllers or farmers. The FMS estates covered 0.25% of the total land area of Britain (Table 2.1). The regional distribution of the 75 estates (Figure 2.1) highlights the non-random nature of the sample. As expected, the majority of estates were from east England (35%) and south-east England (21%), but there were at least two estates sampled from each of the 10 NGC regions. The area of FMS estates in each region highlights this variation (Table 2.1). Most estates were located in very rural areas rather than on the edge of urban areas that might be large enough to support urban fox populations. Though urban foxes tend

to disperse towards rural areas (Page 1981) they disperse over shorter distances than rural foxes, with the mean dispersal distance usually <10 km (Trehwella, Harris & McAllister 1988). This data is therefore likely to be representative of rural foxes with few foxes killed that were born in urban areas.

2.3.2.2 Use of different methods

Between January 1996 and August 2000 a total of 5,655 foxes were killed. The FMS contributors were self-selected as keen users of lamping, accordingly lamping was the most commonly used method for controlling foxes (57%), followed by snaring (13%). The annual mean number of foxes killed per month varied greatly (Figure 2.2), though for methods other than lamping there is no record of the level of effort applied to each. There were two distinct peaks in the annual cull, one in the spring caused by an increase in foxes killed at breeding earths, and one in the summer caused by an increase in foxes killed by lamping. The number of foxes killed by other methods was relatively similar across months.

The regional distribution of method use was less clear, due mainly to the small number of estates in some regions meaning any inference was not representative. Lamping was the most common method in each region (Table 2.2), but estates in different regions put variable resources into culling foxes at breeding earths. The use of snares appears to differ between regions, but the regions showing the extremes in proportional snaring use are also those with only two estates contributing data (W Midlands and NW England).

A more detailed analysis of the lamping data is made possible by the effort data associated with each lamping session, which totalled 15,893 hours of lamping. Analysis was performed by pooling data across estates for each month. Differences in the mean number of foxes killed by lamping each month was not independent of the varied level of lamping effort used each month as the two trends very similar, with the exception of the months September-December where the number of foxes killed dropped off sharper than the number of hours spent lamping (Figure 2.3a, c). The number of foxes killed per month followed a very similar pattern to the number of foxes seen (Figure 2.3b, c), with a mean monthly lamping success (proportion of foxes seen that were successfully shot) of 31% (range 26-40%).

Lamping success was slightly higher in the summer months (May-August), but was relatively constant throughout the rest of the year. Lamping sighting rate (number of foxes seen per hour) peaked in July and August and then showed a steady decline throughout the rest of the year until it began to increase again in June (Figure 2.3d). The sighting rate on individual estates shows a large amount of variation, but on most estates the general pattern of higher values in late summer is apparent (Figure 2.4). Regional mean sighting rate shows a decreasing trend from south to north (Figure 2.5). Mean lamping efficiency (number of foxes killed per hour) followed a similar monthly pattern to sighting rate (Figure 2.3e).

Lamping appears to be a habitual practice for most gamekeepers, with 84% either undertaking one or two sessions per week (mean = 1.61 lamping sessions per week). The timing of lamping sessions followed a seasonal pattern, with sessions starting around 1800 hours during winter months and from about an hour after the fall of darkness in summer months (Figure 2.6). Lamping was typically completed before midnight, except in midsummer.

2.3.2.3 Demographics of foxes killed

Adults and sub-adults (juveniles) made up 80% of the foxes killed. Contributors determined the sex of only 42% of the cubs killed, but these showed an even sex ratio. Contributors determined the sex of a greater proportion (90%) of the older foxes which had a slightly higher proportion of males in the sample, though the sex ratio showed seasonal variation (Figure 2.7). More males were killed during the autumn and winter, with the proportion of females in the cull increasing during the spring.

Of the foxes killed, body parts from 12% ($n=661$) from 30 estates were made available for autopsy. Within those estates that did contribute jaws or carcasses, the mean percentage of foxes provided was only 27% of the total cull on each estate (range 0.5-100%), with only four estates providing >50% of foxes killed. The monthly distribution of date of death for foxes made available for autopsy did not match that of the overall cull, with proportionally more foxes provided during the spring, and fewer provided during the late summer and autumn (Figure 2.8). Analysis of the methods used to kill the foxes provided for

autopsy showed that a smaller proportion of foxes killed by lamping and a greater proportion of foxes killed at breeding earths were in the autopsied sample compared to the total cull (Figure 2.9).

Of the foxes autopsied, 95% had intact canine teeth, with the remainder too damaged by gunshot to be usable. As with other carnivores, the pulp cavities of a fox's teeth fill progressively during the first years of its life, and it is possible to use this feature to distinguish young-of-the-year from older foxes. Using canine teeth, which have a large size, the percentage occlusion of a canine tooth pulp cavity can be measured by first taking a transverse section the tooth along the line of the jaw and measuring the maximum diameter of the pulp cavity and of the tooth at the base of the enamel, then calculating the percentage of tooth diameter that is solid material, i.e. the percentage pulp cavity occlusion (Goddard & Reynolds 1993). Tooth cementum development begins in the autumn following birth and the first dark staining annulus (annual growth line) appears during January to March of the year following birth, after which incremental annuli are used to indicate age (Grue & Jensen 1979; Goddard & Reynolds 1993). Canine teeth <58% occluded have yet to develop the first cementum annuli (Goddard & Reynolds 1993), and by plotting the percentage occlusion against the date of death relative to an assumed mean birth date (April 1; Hewson 1986), it is seen that this percentage corresponds with the time when teeth from the young-of-the-year become of a similar percentage occlusion as adult animals, at about 8 months of age (Figure 2.10). For foxes killed away from breeding earths this percentage occlusion can therefore be used to distinguish between these age groups, despite the maximum percentage occlusion not being reached until foxes are 15-18 months old (Goddard & Reynolds 1993). By using this method, it can be seen that 76% of foxes in the autopsied sample were older animals, i.e. not young-of-the-year. Limited sample sizes prevented further age structure analysis of the FMS dataset as only 87 of the autopsied foxes (13%) were aged to yearly age classes by counting the number of incremental dark-staining lines in the tooth cementum. As these foxes did not represent a random sample, the survivorship curve derived from the data was unreliable as there were far fewer juvenile foxes than would be expected.

By counting the number of placental scars it was possible to estimate the litter size for the 23% of female foxes autopsied that both had intact uteri and were killed between March and July inclusive. Outside of this period the progressive fading of scars makes it difficult to detect them all (Heydon & Reynolds 2000b). The mean litter size was 5.62 ± 0.26 cubs per female (1 s.e., $n=65$). This sample size was too small to allow a comparison between regions. The body weights of foxes killed were contributed for 117 foxes from eight estates. These estates were located throughout Britain so potentially represent the range of body weights observed in Britain. The mean body weight in this sample was 6.50 kg (range 3.17-9.55 kg). 60% of these foxes were male. This mean and range is similar to observations from populations in different parts of Britain (Baker & Harris 2008).

2.4 Discussion

Uniquely, the FMS provides data on how the fox cull responds to variation in both lamping effort and the ability to locate foxes at breeding earths during the year. As with postal questionnaire-type surveys for trapping effort of other species (McDonald & Harris 1999), it was not possible to determine whether this was a representative sample of fox managers, but that seems unlikely. The voluntary nature of the survey is likely to have favoured a proportion of fox managers, i.e. those more likely to keep detailed records of their control efforts, and those who favoured lamping as a control method were especially sought. However, the contributors came from several different types of occupation representing a wide range of management strategies, from those who controlled foxes year-round to those who only put control effort in at certain times of year, and from those who used several different control methods to those who use only their preferred one. The self-selecting nature of the survey meant it was not possible to achieve a regionally representative sample, but the 75 estates still gave widespread coverage across Britain in areas that differ greatly in their reasons for controlling foxes. These diverse reasons included lowland pheasant shooting estates wanting to increase survival of reared birds upon release, to upland grouse moors wanting to increase breeding success, and to farmers wanting to eliminate livestock losses.

By examining mean monthly values and taking Britain as a whole, the FMS identified two periods during which the cull increases, one in spring (March-May) and another in late summer (August-September). Earths are consistently occupied only during the breeding season (Baker & Harris 2008) so an increase in the cull at earths might be expected during the spring when adult foxes can be found near to them. This period coincides with the bird nesting period when fox control to protect ground-nesting birds from predation is often critical, so managers traditionally make a greater effort to control foxes at this time. It is also a time of year when a large impact on the fox population can be made as cubs can be culled before they disperse. FMS contributors recorded the number of occupied earths on an estate, but not the effort used to achieve the cull at earths (time spent locating earths and waiting for foxes to be active near the entrances) so further examination of how much effort was used to achieve the cull at earths is not possible. Foxes were controlled at earths in all NGC regions, but though regional variation in the intensity of fox control at earths in spring has been documented elsewhere (Lloyd 1980; Heydon & Reynolds 2000a), the variable number of estates in each region did not permit comparison between them here.

The number of occupied earths has been suggested as a measure of fox density assuming that each litter represents a social group, but it is an unreliable one (Sadler *et al.* 2004). To convert earth densities to fox densities, uncertain assumptions must be made about adult sex ratios and the proportions of non-breeding females and itinerant foxes in the population (Heydon, Reynolds & Short 2000). Added to this is the problem of accurately censusing earths. Difficulty in distinguishing a currently occupied earth from one recently abandoned can lead to overestimation of earth density, especially in areas where human disturbance causes vixens to move litters frequently, while underestimation can occur in some landscapes as it is difficult to find every available earth, particularly in rocky or densely forested areas. The number of occupied earths is also closely related to food availability (Hewson 1986) and where this is subject to sudden change, i.e. in areas with cyclic rodent populations, foxes can modify their reproductive effort (Lindström 1988), resulting in a lower than expected number of occupied earths.

The other increase in the cull occurs in late summer due to lamping. The influence of seasonal variation in effort on the lamping cull can be examined further due to the unique level of detail about lamping effort the FMS data contain. In absence of effort data, an analysis would suggest the lamping cull increases due to fox density being higher in late summer. With many juvenile foxes that are naive to the threat of man with a spotlight and rifle starting to disperse away from their natal territories, they are easier to shoot. Most juvenile males disperse compared to a lesser proportion of females (Macdonald & Reynolds 2004), which seems a reasonable explanation for the increasing proportion of males in the cull. Though this is undoubtedly a factor, the coincident increase in lamping effort during this period that follows the harvest and removal of cover may also make it easier to see foxes whilst lamping. Lamping efficiency is therefore highest during late summer as there is a larger pool of foxes that are easy to detect. An increase in lamping effort also occurred during the spring, presumably due to managers attempting to reduce predation during the nesting season, but the fox cull did not respond to this. This is both because there are fewer foxes left to shoot following a winter of culling and that previous experience of being shot at and surviving is likely to have induced some avoidance behaviour (lamp shyness) in foxes. These two factors result in lamping efficiency remaining low. Since the FMS survey, the development of low-cost night-vision optics is likely to have led to improved efficiency at this time of year as spotlights do not need to be used as frequently.

Compared to the number of foxes culled within a time interval, the sighting rate of foxes is a more useful index of fox density because it accounts for changes in effort over time. It is therefore equivalent to the catch per unit effort that has long been used both as an abundance index and to estimate abundance (Seber 1982), but indexes the target population and not the attempt to control it. The sighting rate of foxes on spotlight counts has often been used as an index of relative abundance (Sadler *et al.* 2004) as it has been shown to agree closely with estimated fox density (Heydon, Reynolds & Short 2000). The mean sighting rate pooled across estates shows a similar seasonal trend to the fox cull, but the coincidental trend in effort with the number of foxes seen means that there is less variation in the sighting rate compared to the fox cull, and the trend is smoother. The changes in sighting rate during the year that are seen on most estates would appear to reflect the general

biological processes that cause changes in population density, reproduction in the spring causing it to increase in the summer once cubs become independent of the breeding earth and therefore visible while lamping (Baker & Harris 2008), followed by mortality during the autumn and winter that result in a gradual decline. This seasonal trend was confirmed on a regional-scale by a study that surveyed fox populations in autumn and spring (Heydon, Reynolds & Short 2000). The regional north-south trend broadly matches known density estimates based upon landscape types that dominate the different regions (Webbon, Baker & Harris 2004), though the sighting rate in East Anglia was higher than expected compared to other regions in England (Heydon, Reynolds & Short 2000).

The use of sighting rate as an index of abundance implies assumptions about the nature of the relationship between sighting rate and fox population density. In addition to being constant over time, this relationship is often assumed to have a linear form. In this form, the slope parameter is known as detectability, or the proportion of the population seen per unit of effort. The relationship can in fact take on two other forms, a hyperstable form where the rate stays high as density drops, i.e. foxes become easier to see the fewer there are, or a hyperdepleted form where the rate drops much faster than density, i.e. foxes become harder to see the fewer there are (see Fig. 5.2 in Hilborn & Walters 1992). The latter of these forms is possible, especially as the remaining foxes in the population after a period of lamping effort are likely to be lamp-shy. Given a lack of data on seasonal farming practices on estates, the assumption of constant sightability during the year is likely to cause problems on estates where grass and crop cover change significantly during the year as it seems reasonable that sightability would be lower when cover is high, i.e. during the spring/summer growing season. At a larger scale this might suggest that sightability could vary by region or landscape. Sightability could also be affected by features of fox behaviour. The sighting rate shows a small increase during December and January that, barring a large immigration event occurring on all estates, is unlikely to be due to a population increase. One possible explanation is behavioural changes during the mating season that might result in foxes being less wary of lamps and so easier to detect (as they are distracted). To determine the exact form of this relationship would require long-term field study. This would require constant monitoring of the sighting rate during different seasons, with the use of tagging or similar

methods to estimate density together with culling (by methods other than lamping to avoid lamp-shyness) to reduce the density by a known amount.

Detailed analysis of the snaring cull was not possible due to the lack of data on snaring effort (number of snares set per day). The cull from snaring was relatively constant throughout the year, though a lower proportion of the snaring cull was achieved in February and March. Snaring is most successful when there is cover in the form of crops or tall grass in which to disguise snares. Though the conditions for successful snaring vary greatly during the year, it has been found that though the use of snares varies greatly between gamekeepers, the difference in seasonal use of those that do is less than might be expected based upon the difference in conditions, i.e. gamekeepers use a similar number of snares throughout the year (GWCT, unpublished data). Assuming a similar pattern in FMS contributors' effort means that snaring efficiency (foxes killed per snare) is lowest in the early spring, which coincides with when cover is at its most sparse. However, early spring is also when lamping is least efficient and so low culling efficiency at this time of year is likely to be due to a combination of factors that reduce the number of foxes to be caught in snares or seen when lamping, which include: (1) reduced fox population density at this time of year following over-winter mortality, (2) increased territoriality of foxes during this period reducing the likelihood of itinerant foxes being present, and (3) the relative inactivity of nursing vixens prior to and after birth (Lloyd 1980). This highlights the potential importance of controlling foxes at breeding earths during this time of year.

The FMS contains an unprecedented amount of data on rural fox control effort across Britain, with the level of detail on lamping from individual estates making it very useful for modelling local scale population dynamics. However, despite the quantity of information, the voluntary nature of the survey means that it does have some flaws. These include the lack of regional representation in the data and the variation in length of contribution, which appears to decrease south-north. The time and discipline required by managers to record data every day was not insignificant, which most likely explains why the number of estates contributing complete record book sets from January 1996 to August 2000 was relatively small. The additional effort required to collect fox carcasses was clearly too great for many

contributors, meaning that the autopsied sample of foxes reflected the managers ease of carcass collection rather than a random sample. Foxes killed by lamping are more difficult to recover as they are often shot from several hundred feet away, as shown by the low number of foxes killed by lamping during autumn and winter in the autopsied sample. This meant that younger foxes were under-represented in the sample and so the age structure determined by the FMS was unreliable. The collection rate might have been improved by using some form of incentive scheme to encourage collection of killed foxes, but given the large number of foxes culled this would have been prohibitively expensive.

Prior to the FMS, the data available on rural fox populations in Britain was not of sufficient spatial or temporal resolution to allow modelling of the within-year population dynamics on estates. The lack of data on culling effort further limited the potential modelling options. At this time, gamekeepers would commonly evaluate their fox control efforts simply by the numbers of foxes killed in one year, i.e. fox bag data such as that forming part of the NGC, and comparing this bag to their fox bag in previous years and with their peers. They would also consider the size of game bags that were achieved. In the year before the FMS started (1995), the mean number of foxes killed on an estate was just over 3 foxes $\text{km}^{-2} \text{yr}^{-1}$ (range 0-36 foxes $\text{km}^{-2} \text{yr}^{-1}$, Figure 2.11). The fox bags on 50% of the estates were fewer than 2 foxes $\text{km}^{-2} \text{yr}^{-1}$. Gamekeepers might therefore argue, as a rule of thumb, that if they had removed more than this number of foxes, their fox control was relatively effective. Since 1995, a number of predator removal studies have demonstrated that fox control can reduce fox density and achieved positive effects on game and other ground-nesting bird species by removal of large fox bags of over 5 fox $\text{km}^{-2} \text{yr}^{-1}$ (Stoate & Leake 2002; Fletcher *et al.* 2010; Potts 2012), although others have achieved success with smaller bags of closer to 2 fox $\text{km}^{-2} \text{yr}^{-1}$ (Tapper, Potts & Brockless 1996). These studies serve to reinforce the rule of thumb that a bag of more than 2 foxes $\text{km}^{-2} \text{yr}^{-1}$ was an indicator of effective fox control on their estate.

On average, gamekeepers might therefore appear to be successfully controlling fox density using the rule-of-thumb. Larger bags, in this understanding, would result from repeated replacement of culled foxes through immigration over the course of the year.

However, given a fox density of 1 fox km⁻² (i.e., within the range of regional and landscape scale estimates; Heydon, Reynolds & Short 2000; Webbon, Baker & Harris 2004) and annual productivity of three cubs per fox, a bag of 3 foxes km⁻² yr⁻¹ is comparable only with annual productivity, without invoking immigration from outside the estate. An annual cull of this magnitude is therefore on the scale of a sustainable harvest rather than the overwhelming mortality likely to control the population. In the absence of an understanding about the effect of control on fox density on each restricted area estate within the year, the conclusion would be that control on most estates was actually failing to effectively reduce fox density.

Of course, local differences in fox density, timing of the cull, and rate of replacement make this an incorrect conclusion. If foxes are prevented from breeding locally, and are not rapidly replaced by immigration, culling at this level might be effective in reducing fox density. This example further highlights the problems in using bag data to indicate success when there is no measure of culling effort or any indicator of fox density. If there are few foxes to remove then the bag can only be small, even with high levels of control effort; the local fox population may nevertheless be strongly suppressed and the cull achieving its objectives. It is therefore necessary to understand how fox density changes in response to culling effort. The difficulty of estimating fox density on short time-steps using field methods means that this is only possible using population dynamics modelling. The importance of the FMS in bridging the gap in data between intensive local studies and long-term survey schemes to provide fox sighting rate data for modelling fox populations at local scales therefore cannot be understated.

2.5 Tables

Table 2.1. The National Gamebag Census regional classification (Tapper 1992), detailing regional area and the proportion of each of these regions that Fox Monitoring Scheme estates covered.

Name (code)	Counties	Area (km ²)	FMS estates	FMS area [km ² (%)]
SW England (1)	Avon, Cornwall, Devon, Dorset, Somerset	17,720	7	41.3 (0.23)
SE England (2)	Berkshire, E Sussex, Hampshire, Kent, Middlesex, Surrey, W Sussex, Wiltshire	19,680	16	64.9 (0.33)
E England (3)	Cambridgeshire, Essex, Lincolnshire, Norfolk, Suffolk	22,170	26	197 (0.89)
C England (4)	Bedfordshire, Buckinghamshire, Hertfordshire, Leicestershire, Northamptonshire, Nottinghamshire, Oxfordshire, Warwickshire	16,360	5	35.2 (0.22)
W Midlands (5)	Gloucestershire, Hereford & Worcester, Shropshire, Staffordshire, W Midlands	13,690	2	21.9 (0.16)
Wales (6)	All	20,760	3	36.9 (0.18)
NW England (7)	Cumbria, Cheshire, Greater Manchester, Lancashire, Merseyside	16,810	2	13.0 (0.08)
NE England (8)	Cleveland, Durham, Humberside, N Yorkshire, Northumberland, S Yorkshire, Tyne & Wear, W Yorkshire	23,960	7	52.6 (0.22)
E Scotland (9)	Borders, Central, Fife, Grampian, Lothian, Tayside	26,740	3	58.5 (0.22)
W Scotland* (10)	Dumfries & Galloway, Highland, Strathclyde	41,300	4	13.8 (0.03)

*area excludes the Orkney Islands, Shetland Islands and Western Isles of Scotland as foxes are absent from these areas (Harris *et al.* 1995)

Table 2.2. Percentages of the total cull across FMS estates in each of the NGC regions made by different methods. (N.B. some rows do not sum exactly to 100% due to rounding error)

Region	Lamping (%)	Snaring (%)	Earth – adults (%)	Earth – cubs (%)	Drives and traps (%)	Other (%)	Number of estates
SW England	54.5	10.5	1.2	7.9	2.0	23.8	7
SE England	73.8	6.6	0.5	2.3	6.4	10.4	16
E England	61.0	10.2	2.0	10.9	5.0	11.0	26
E Midlands	60.1	13.3	0.3	5.7	3.8	16.8	5
W Midlands	57.9	1.1	2.1	12.6	10.5	15.8	2
Wales	59.8	10.8	3.9	12.7	1.0	11.8	3
NW England	41.4	31.2	9.6	7.0	8.3	2.5	2
NE England	61.9	8.5	2.6	7.5	1.6	17.9	7
E Scotland	36.5	23.9	5.3	22.8	3.3	8.1	3
W Scotland	76.2	8.9	1.0	4.0	0.0	9.9	4

2.6 Figures

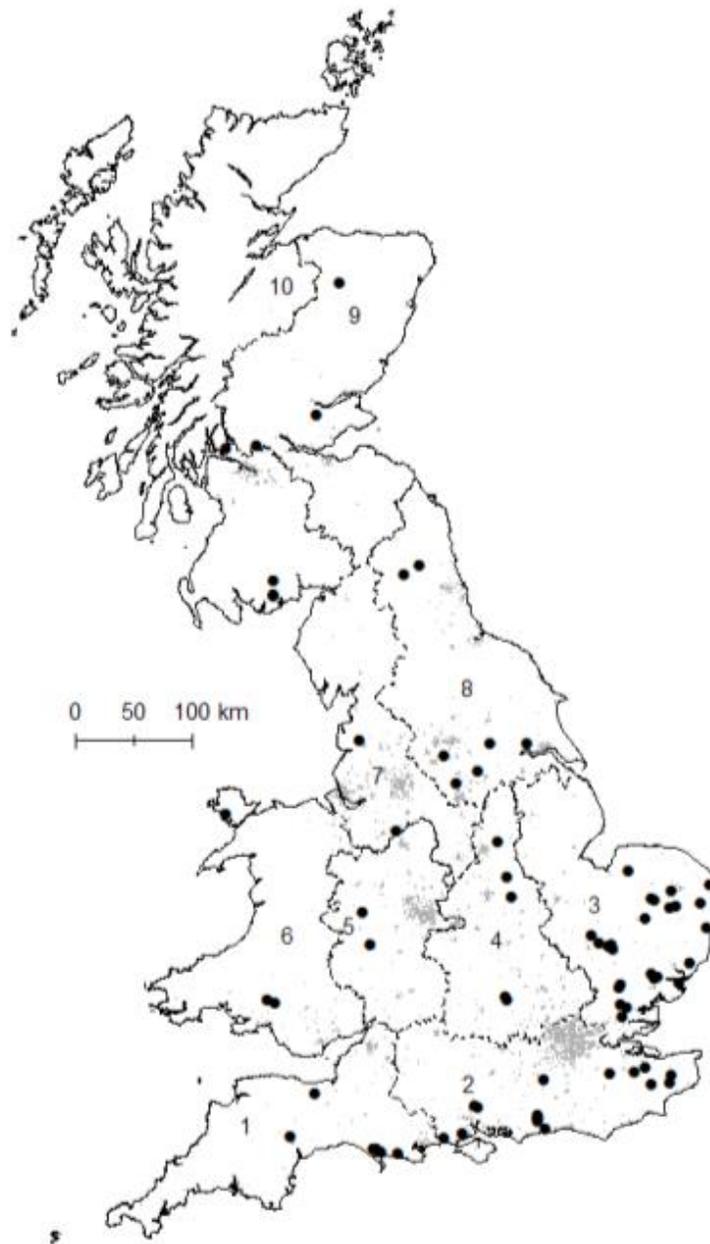


Figure 2.1. Map of Great Britain showing the location (filled black circles) of the 75 rural estates that contributed data to the Fox Monitoring Scheme between January 1996 and August 2000. National Gamebag Census regions (dashed lines) are shown (1 = SW England; 2 = SE England; 3 = E England; 4 = C England; 5 = W Midlands; 6 = Wales; 7 = NW England; 8 = NE England; 9 = E Scotland; 10 = W Scotland). Urban areas (grey 1-km squares) were identified based upon the dominant land classification in each 1-km square from the Countryside Survey 2000 dataset using the Countryside Information System (CEH 2005).

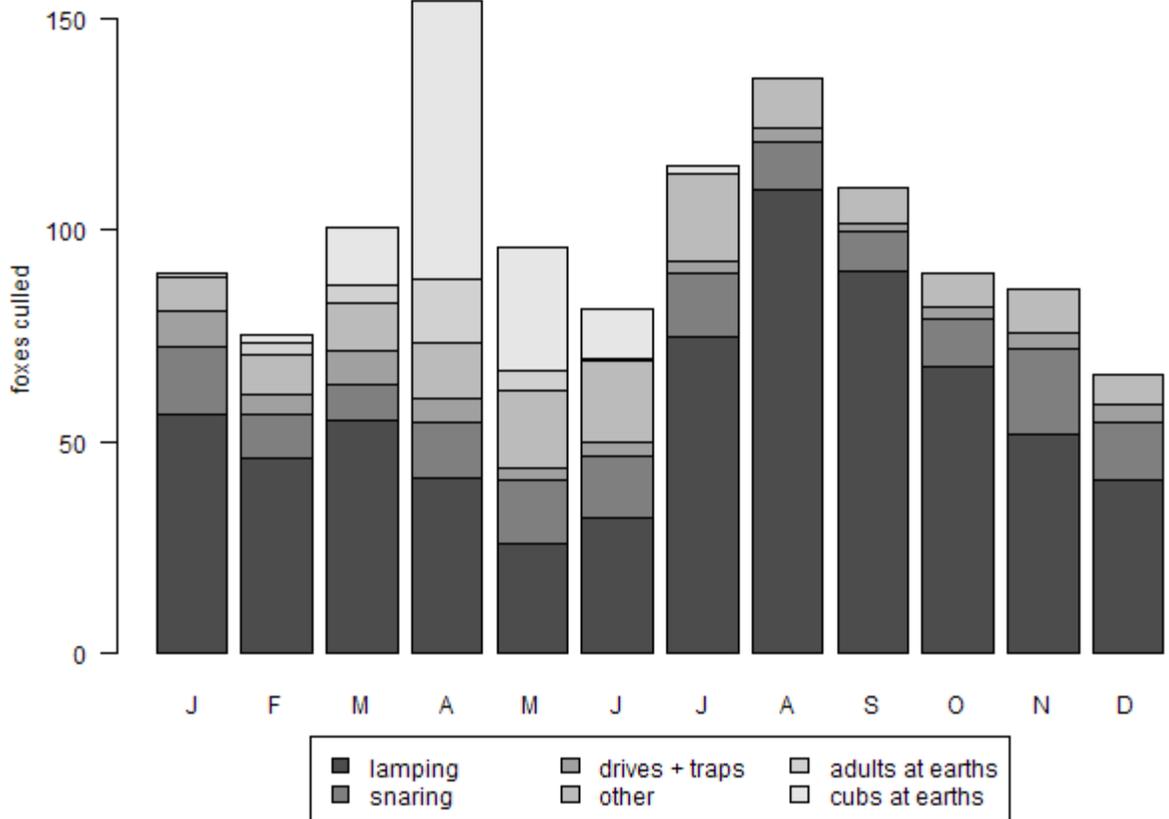


Figure 2.2. Monthly variation in mean annual number of foxes killed (pooled across estates) showing the composition of the cull by different control methods.

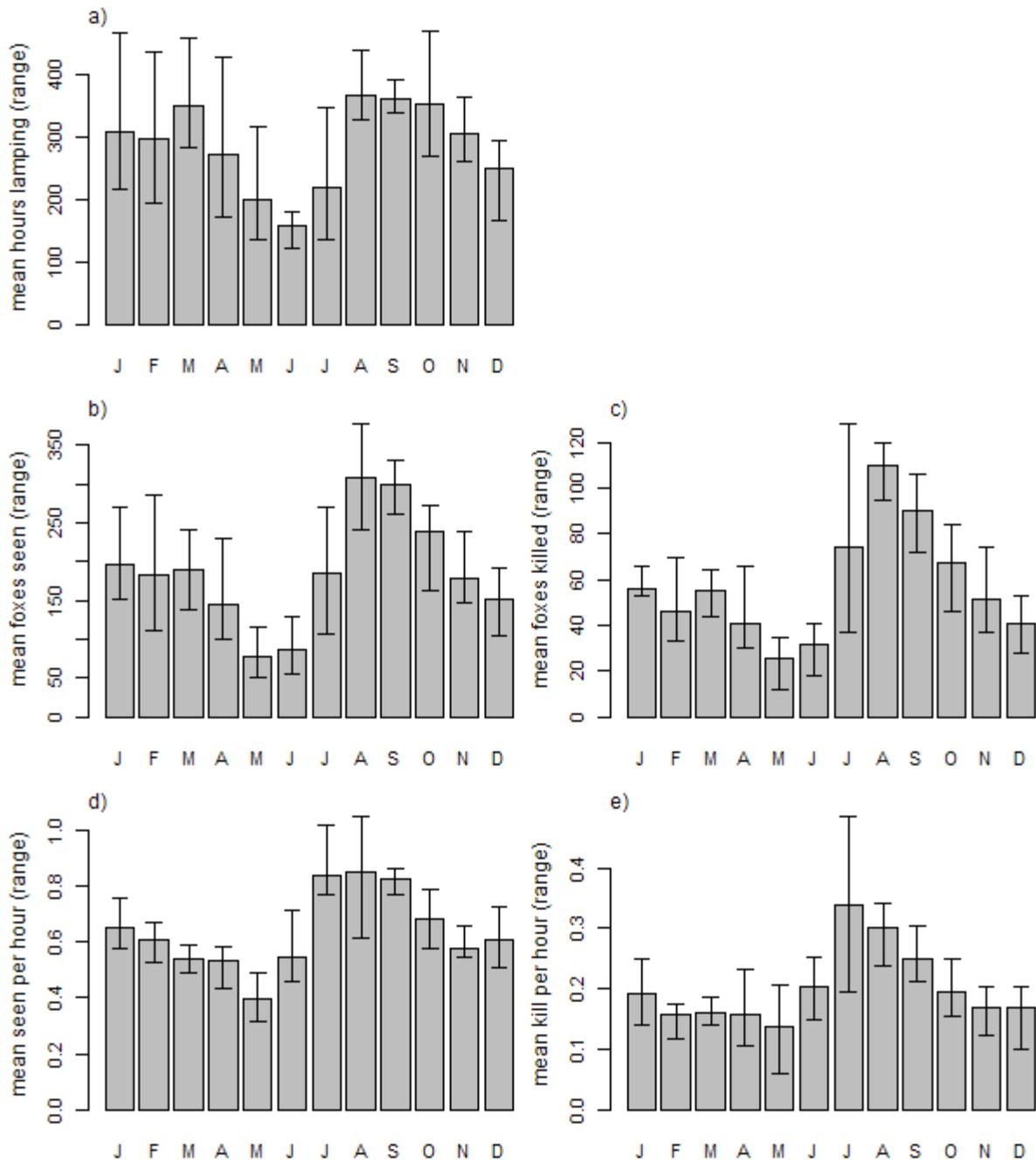


Figure 2.3. Monthly variation in mean annual lamping data pooled across estates, showing a) the number of hours spent lamping; b) the number of foxes seen; c) the number of foxes killed; d) the number of foxes seen per hour (sighting rate); e) the number of foxes killed per hour (efficiency).

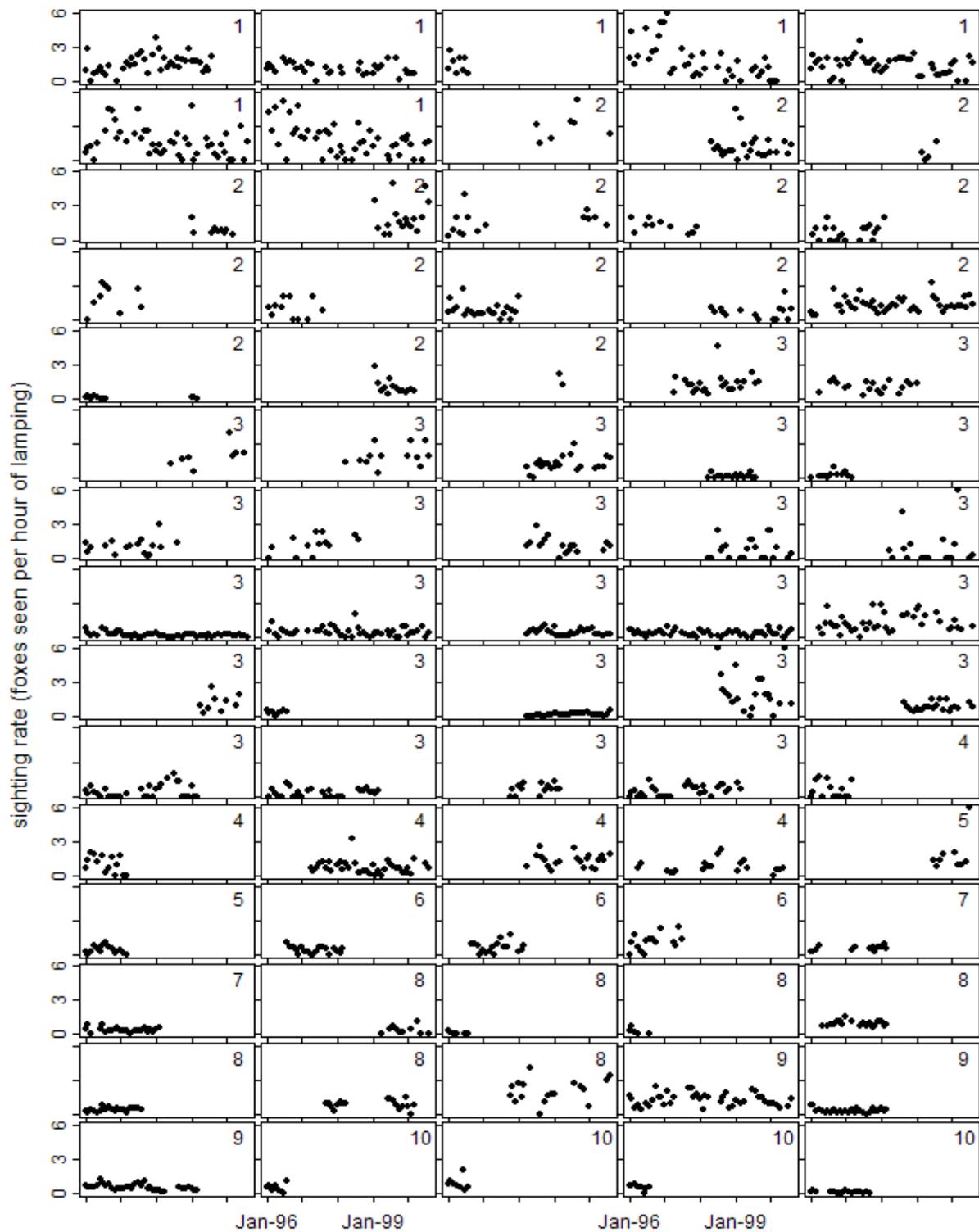


Figure 2.4. Monthly sighting rate of foxes on FMS estates between January 1996 and August 2000. Estates are labelled by NGC region code (see Figure 2.1), data are all shown on the same scale for comparison. Blank months indicate either no contribution or zero lamping effort.

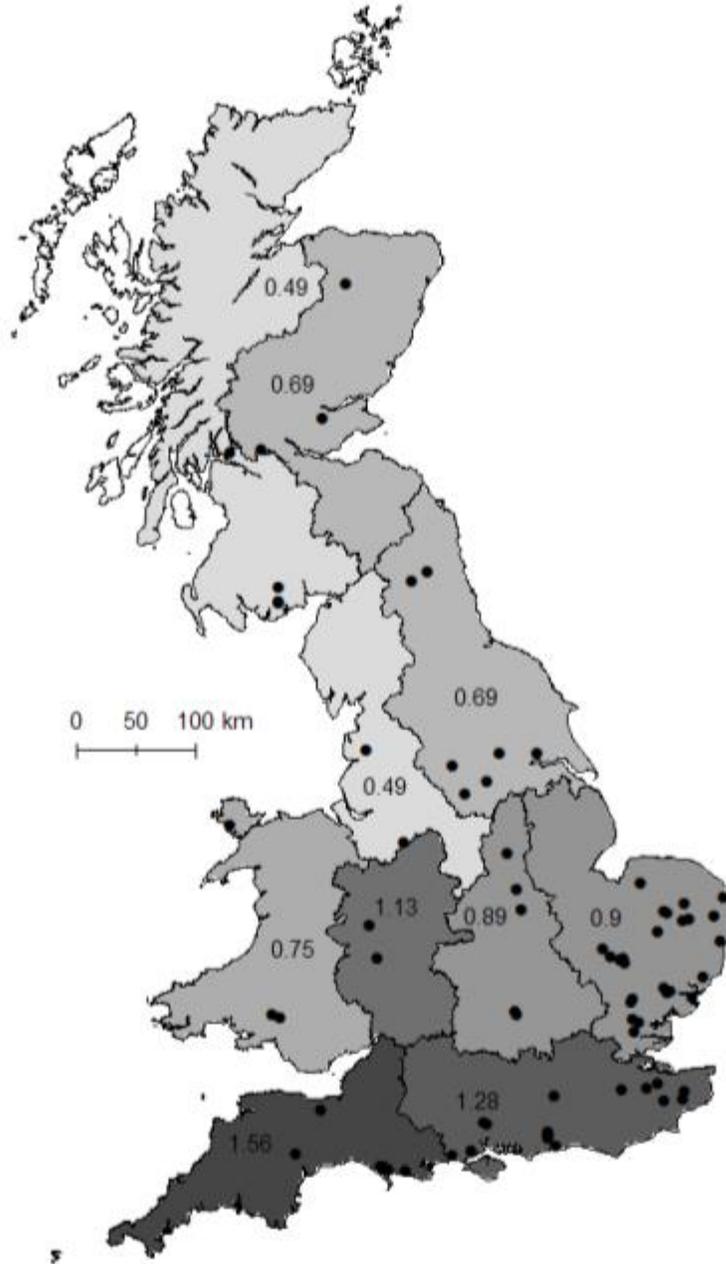


Figure 2.5. FMS estates (filled black circles) showing the regional mean annual sighting rates (foxes seen per hour of lamping) across estates. Greyscale shows sighting rate from low (light) to high (dark). White indicates no data as foxes absent from these islands.

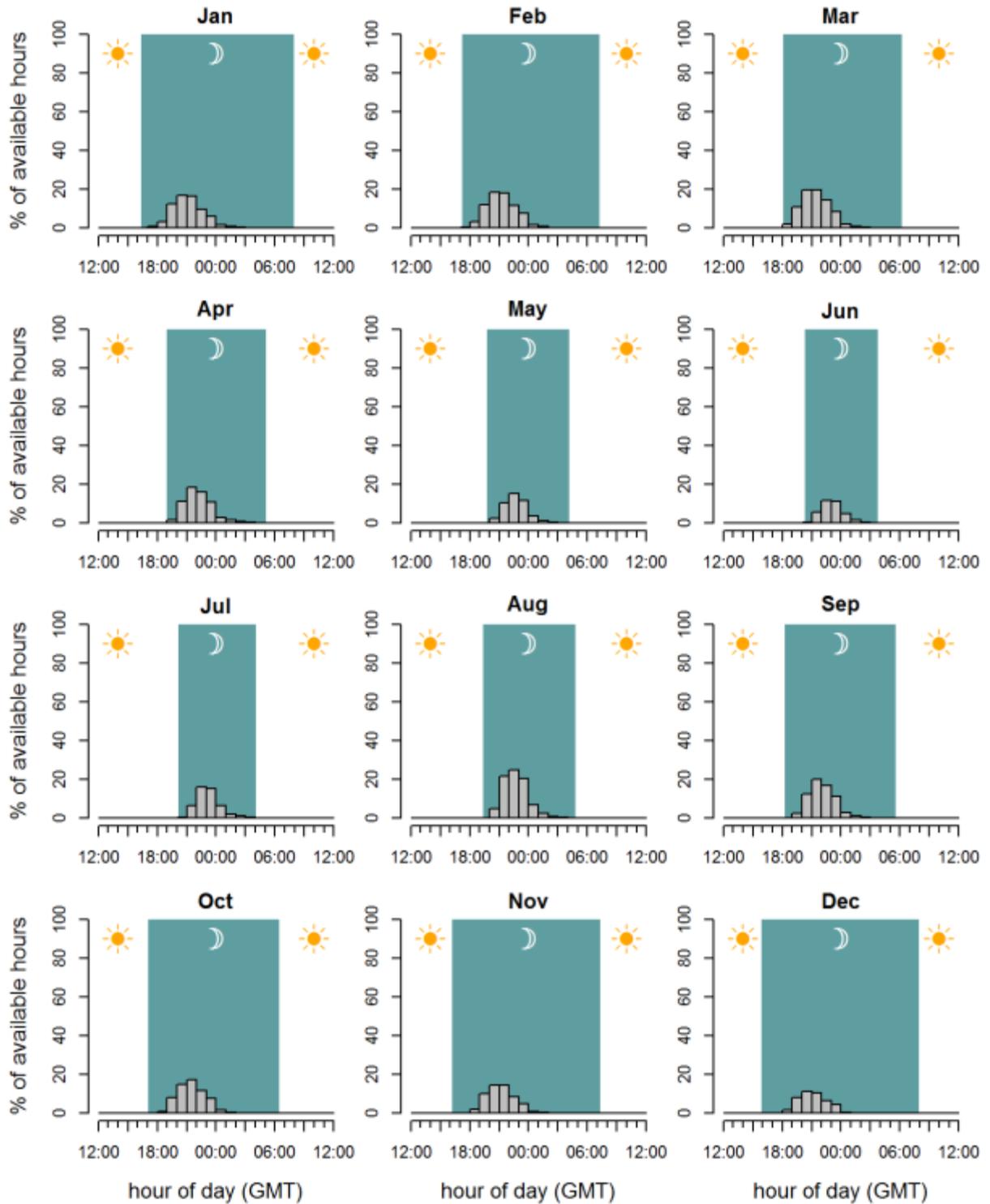


Figure 2.6. Timing of lamping hours used relative to the hours of darkness in each month.

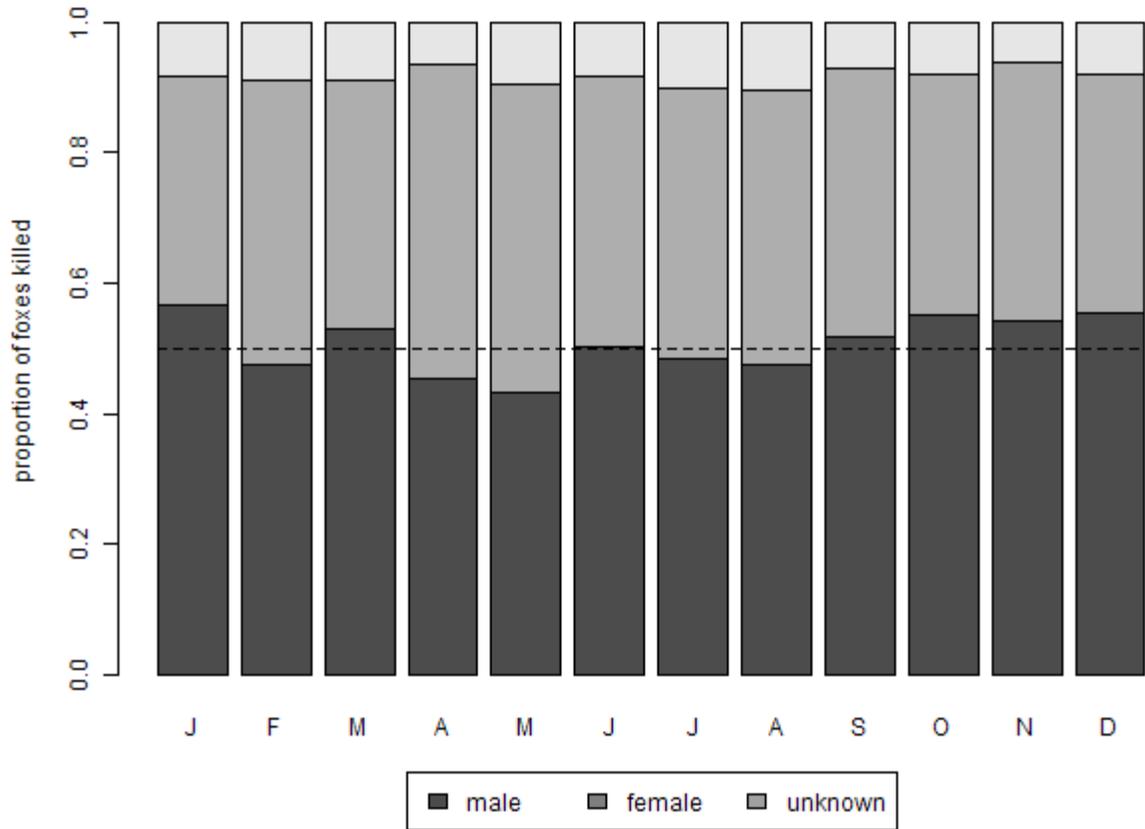


Figure 2.7. Sex ratio of the 4547 adult and juvenile foxes culled across 75 estates between January 1996 and August 2000.

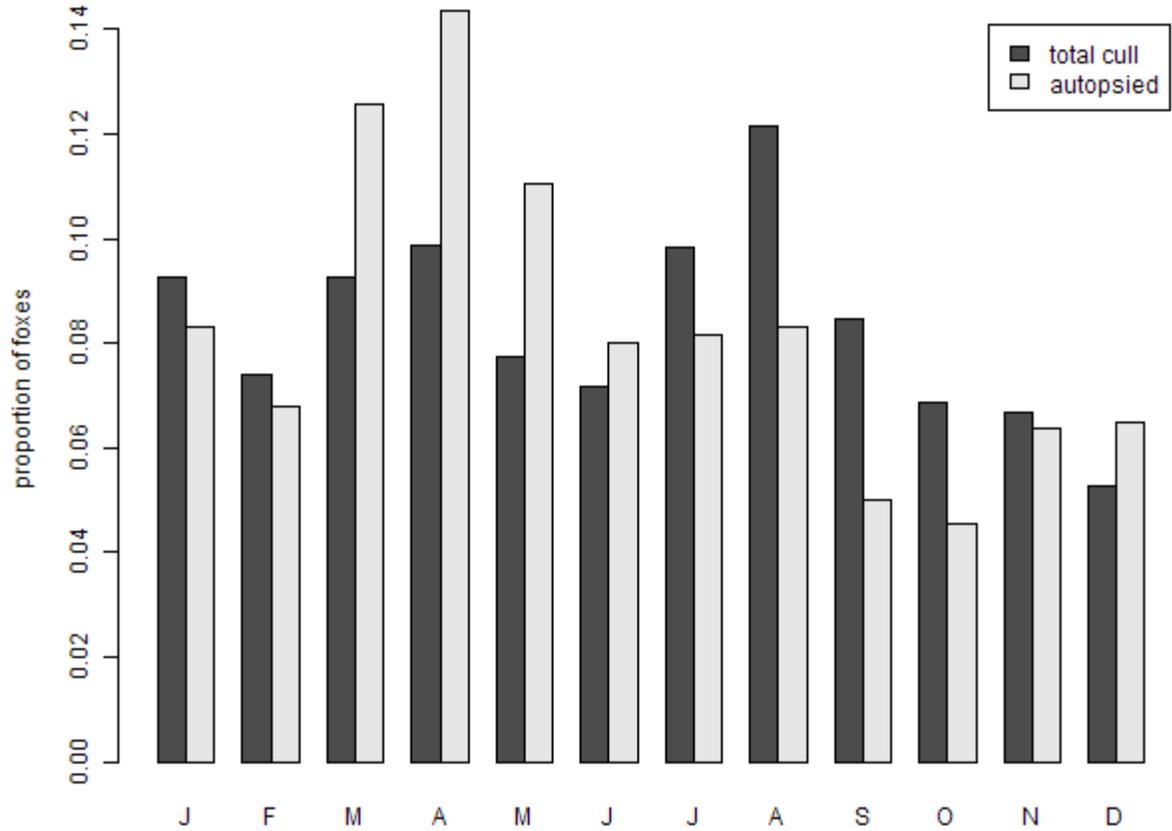


Figure 2.8. Comparison of the monthly distribution of the total fox cull and the sample made available for autopsy by contributors.

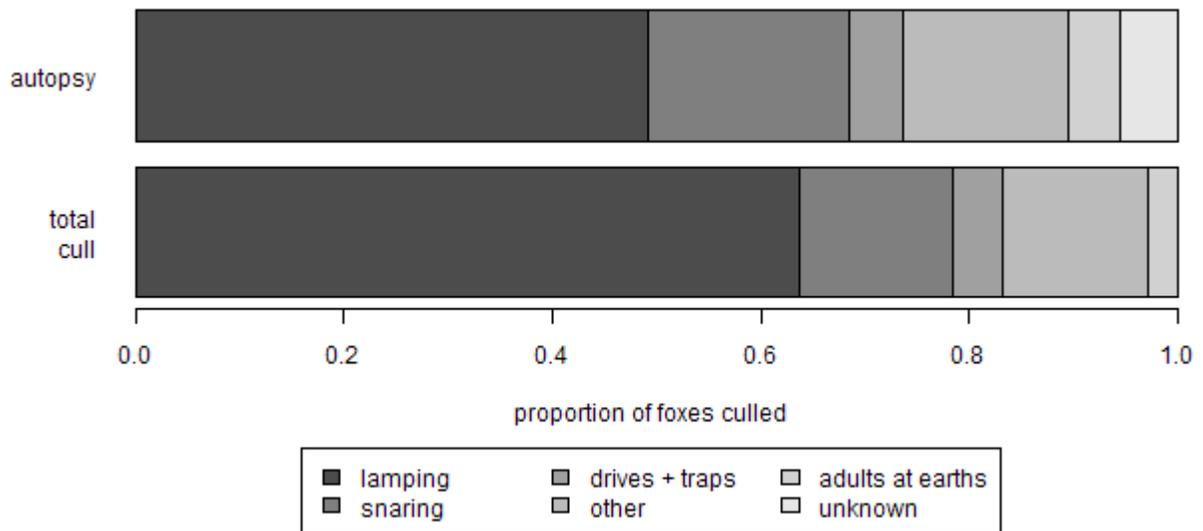


Figure 2.9. Comparison of the proportional use of different methods used to kill foxes between the total cull and the sample made available for autopsy by FMS contributors.

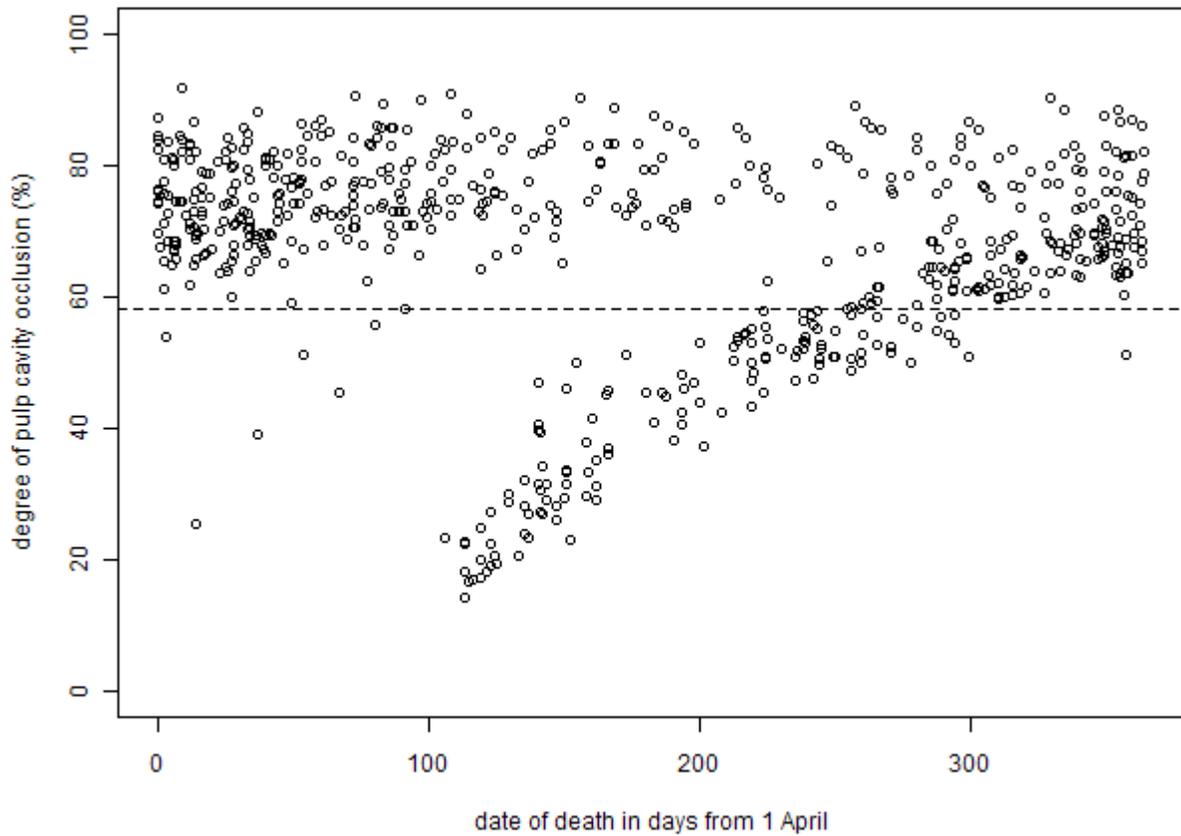


Figure 2.10. Percentage occlusion of fox canine teeth pulp cavities as a function of the date of death in days from an assumed mean birth date of 1 April. Dashed line indicates the percentage occlusion below which canine teeth are yet to develop the first cementum annuli.

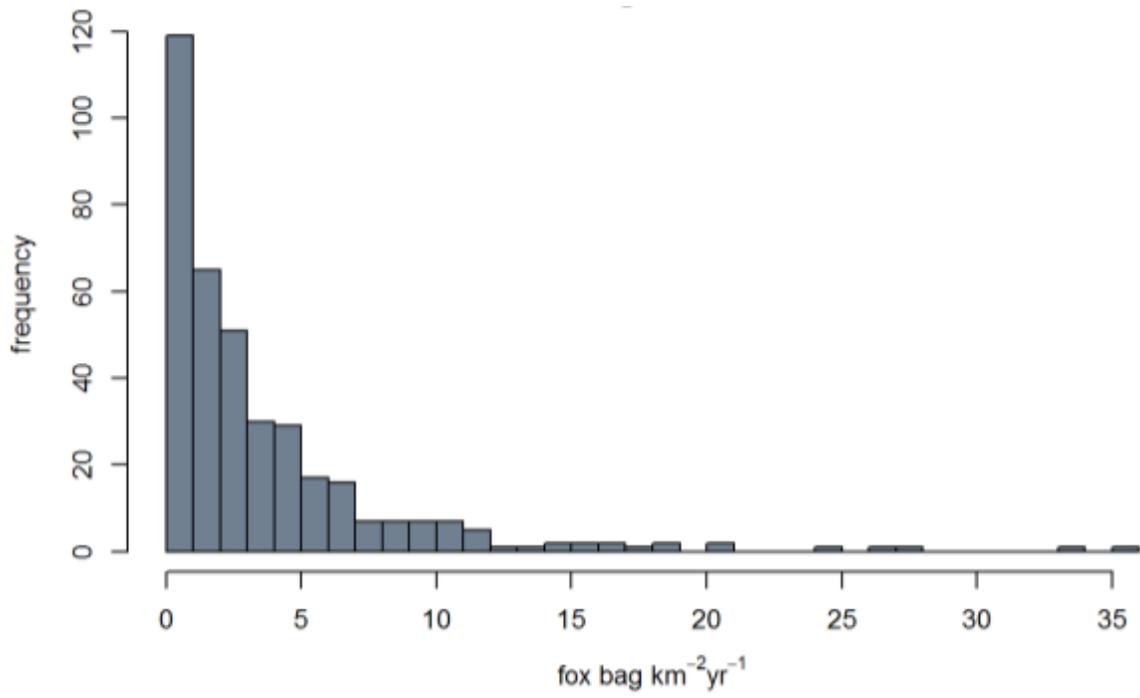


Figure 2.11. Data from the National Gamebag Census on the numbers of foxes killed on shooting estates in 1995.

Chapter 3: Modelling local-scale fox population dynamics: a simulation-estimation study

3.1 Introduction

3.1.1 Why model fox populations?

Red fox (*Vulpes vulpes*) populations in rural Britain have been managed by culling for centuries (Reynolds & Tapper 1996; Baker & Harris 2008). In fox populations subject to culling, demographic studies have suggested that this deliberate killing of foxes by man is a significant cause of fox mortality in both rural and urban areas (Harris & Smith 1987; Heydon & Reynolds 2000a). Fox ecology has been widely studied (Lloyd 1980; Macdonald & Reynolds 2004; Baker & Harris 2008) but, despite decades of work, the effects of different fox culling strategies on rural fox population densities and demographic parameters have not been well-examined (Devenish-Nelson *et al.* 2013). This is because most studies have attempted to determine the impact of fox culling indirectly on prey populations, rather than directly on fox populations (Baker & Harris 2006). Predator control is increasingly subject to public scrutiny, and a scientific evaluation of the potential effectiveness and ecological outcomes of culling is needed (Fall & Jackson 2002). Determining that lethal control is effective at reducing the fox population density and thereby fox predation on livestock, game and species of conservation concern is a key part of that evaluation, together with understanding the specificity and cost-effectiveness of the culling efforts (Baker & Harris 2006).

In Britain, crude assessments of the impact of fox culling at the national scale have all concluded that estimates of the total annual cull could easily be met by productivity in the fox population (i.e. the number of cubs born annually, Reynolds & Tapper 1996). Rather than reducing the number of foxes and achieving population control, this suggests that at this scale the fox population is being maintained at a productive level by culling. Fox culling is performed at local scales (< 50 km²) by individual gamekeepers, farmers and reserve wardens (referred to collectively as gamekeepers hereafter). There is minimal coordination

of culling effort across the landscape, and foxes on a large proportion of landholdings (57%) are not under any form of control (Defra 2012). Such heterogeneous culling effort means that the impact of culling on local fox populations may vary greatly depending on the level of neighbouring control. In restricted-area culling, replacement of culled individuals on some time scale by immigration is inevitable. The impact of culling on local fox density is related to the fox density in surrounding areas, as culling creates population sinks that can be rapidly filled by immigration (Kinnear, Onus & Bromilow 1988; Reynolds, Goddard & Brockless 1993; Thomson *et al.* 2000; Baker & Harris 2006). The existence of many local sinks due to a generally high intensity of culling at regional scales ($> 1000 \text{ km}^2$) can result in suppressed regional fox density (Heydon & Reynolds 2000a; b). While this suggests that collaboration between neighbouring gamekeepers might be an effective strategy to reduce regional fox density, the impact of culling must be determined at the local scale if individual gamekeepers are to evaluate their own culling effort and develop more effective management strategies for their local situation. Estimation of fox density and demographic parameters at the local scale is therefore required.

Field studies to estimate fox density and demographic parameters, e.g., using mark-recapture methods, require a level of effort typically unavailable to gamekeepers and are inappropriate in the fast-changing context of intensive culling. In absence of monitoring data there is limited scope for gamekeepers to assess the effect of past culling actions, meaning culling strategy is based upon rules-of-thumb derived from personal or collective experience. Such working rules provide no indication of effectiveness in the immediate case. Nevertheless, gamekeepers do in fact have quite a lot of local and time-specific information available to them, especially as a result of culling actions which can be seen as informative perturbations. As described in Chapter 2, the Fox Monitoring Scheme (FMS) was set up to collect such data systematically. The purpose of this thesis is to explore how mathematical models can make use of such data to give a quantitative understanding of local fox dynamics during the culling process, and evaluate its effectiveness. Exploratory models can also be used as “What if...” tools to predict the likely impact of different culling actions (Buckland *et al.* 2007) and identify ways to increase effectiveness. By using monitoring data to update the models retrospectively to determine whether predicted impacts were achieved, the

models can be improved iteratively through the use of adaptive management techniques (Walters 1986). A fox population dynamics model incorporating the key demographic processes acting at the local scale is therefore required to formulate effective fox management strategies.

3.1.2 Fox ecology: background

Formulation of a model for foxes requires an understanding of fox ecology to determine which demographic processes are important at the local scale. The fox population on an estate will be subject to 1) mortality from culling and non-culling factors, 2) reproduction by resident foxes, and 3) immigration onto, and emigration off of, the estate. Each of these processes might be expected to vary with respect to fox density, sex, age, and time, but incorporation of all such relationships would likely result in an over-parameterised model that could not be identifiable using the available data, i.e. the parameters could not all be reliably estimated from the data. Some justification of the assumptions made about each process in the model formulated below is given here. [N.B. across its range, the red fox is notable for flexibility in its habits (Voigt & Macdonald 1984), so where possible the information summarised here pertains only to rural British fox populations.]

3.1.2.1 Fox mortality

Foxes in Britain are at risk from various mortality factors, among which culling can be the dominant cause of mortality even at a regional scale (Heydon & Reynolds 2000a; b). Culling mortality factors have been shown to be a substantial additive component of overall fox mortality as overall mortality rates are higher where culling is more intense (Heydon & Reynolds 2000b). Non-culling mortality factors may also be important in determining local fox densities. These include natural risks from disease, predation, starvation, accidents or inclement weather, and non-natural risks from road traffic collisions and secondary poisoning. Foxes have few natural predators in Britain, although where present golden eagles (*Aquila chrysaetos*) may kill both cubs and adults, and badgers (*Meles meles*) and domesticated cats and dogs may kill cubs (Macdonald & Reynolds 2004; Baker & Harris 2008). British foxes are exposed to fewer disease mortality risks than European foxes, with

rabies absent (Holmala & Kauhala 2006) and fewer parasites present (Baker & Harris 2008). The most prevalent parasite is the skin-dwelling mite (*Sarcoptes scabiei* var. *vulpes*) that causes sarcoptic mange. Information on mange in rural populations is limited, but outbreaks of mange in high density urban populations can dramatically reduce fox density (Lindström 1992; Soulsbury *et al.* 2007). Other diseases, e.g., parvovirus, do not appear to cause significant fox mortality (Macdonald & Reynolds 2004; Baker & Harris 2008). Road traffic collisions may be a locally important mortality factor where road traffic is a dominant landscape feature, such as in urban areas (Macdonald & Reynolds 2004). The local risk in rural areas is unknown but is expected to be lower and also seasonal due to dispersal. At regional scales it has been shown that rural fox density does not match variation in road density, suggesting that it is not a major determinant of fox density at this scale (Heydon & Reynolds 2000b).

Considerations when modelling mortality rates include 1) whether the risks are similar for all age classes, 2) whether the risks remain constant over time, and 3) whether the risks are density-dependent. Culling mortality might be expected to have a differential impact on various age classes, as few older foxes are found in areas with intensive fox culling (Lloyd 1980; Hewson 1986; Heydon & Reynolds 2000b), and juvenile foxes have been shown to be more at risk from culling than adult foxes (Englund 1970; Pils & Martin 1978; Heydon & Reynolds 2000b). This is consistent with mortality rate showing a U-shaped relationship with age (Caughley 1977). High juvenile mortality from non-culling mortality factors, e.g. road traffic collisions, will also contribute to this relationship (Storm *et al.* 1976; Macdonald & Reynolds 2004; Baker *et al.* 2007). In addition to being more naïve with respect to culling methods (Reynolds 2000), juvenile foxes are more likely to disperse than older foxes (Macdonald & Reynolds 2004; Baker & Harris 2008), putting them at greater risk of both culling and non-culling mortality factors (Marcström 1968; Harris & Trehwella 1988; Reynolds 2000). Contrarily, recent evidence suggests that mortality rates are not measurably higher for dispersing foxes (Soulsbury *et al.* 2008). Without age-structured data it is not possible to estimate age-specific mortality rates, so the assumption made here was that non-culling mortality rates were age-independent.

When the number of foxes killed in each time period is known, as in the FMS data (Chapter 2), changes in culling mortality rates over time are accounted for directly by conditioning the model on the cull and removing those foxes killed from the modelled population at each time step. However, non-culling mortality rates must usually be assumed constant over time due to the vast data requirements to estimate them as time-dependent parameters, e.g. from long-term tagging experiments (Hilborn & Walters 1992). Given the data available from the FMS, non-culling mortality rates were therefore assumed to be constant.

Conditioning the model on the cull also means modelling density-dependence in culling mortality rates is not necessary. Density-dependence is expected in non-culling mortality rates, as a fox population at high density relative to carrying capacity is expected to be at increased risk from extrinsic factors such as disease and starvation due to increased transmission rates and reduced food availability, respectively. For populations subjected to historic and ongoing culling mortality, it is reasonable to assume that density will not generally be close enough to carrying capacity for such density-dependent effects to occur. Additionally, other important non-culling mortality factors, such as road traffic collisions, are considered to be density-independent. It is important to note that parameterising non-culling mortality rate with a density-independent term does not mean that density-dependent effects are absent from the model; instead they are mediated through other processes in a model, e.g. reproduction and immigration.

3.1.2.2 Fox reproduction

Adult red foxes establish and hold territories either as male/female pairs or as extended social groups in which a dominant male/female pair tolerate other subordinate individuals, which are typically related non-breeding ‘helper’ females (Macdonald 1979; Reynolds & Tapper 1995a). The home ranges of members of a social group overlap widely with each other, but there is little overlap between neighbouring groups due to the territory structure (Macdonald 1979, 1980a). Home range size varies widely among habitats; in rural Britain estimates range from 2.3 km² in arable Oxfordshire to 40 km² in the uplands of Scotland (Voigt & Macdonald 1984; Hewson 1986; Reynolds & Tapper 1995a; Baker &

Harris 2008). In contrast, extremely small home ranges of $<0.4 \text{ km}^2$ are not uncommon in urban areas where food availability is greater (Harris 1980; Doncaster & Macdonald 1991; White, Saunders & Harris 1996; Baker *et al.* 2000). There is no relationship between territory size and group size (Macdonald 1981, 1983; but see Baker *et al.* 2000), but the proportion of breeding females in the group, and litter size, varies with food availability (Voigt & Macdonald 1984). Fox prey abundance has been shown to vary predictably between habitats (Macdonald, Bunce & Bacon 1981), suggesting that productivity may depend upon habitat. Socially-mediated suppression of reproduction also occurs amongst females, meaning that even when food is unlimited, social status can lead to only dominant females breeding (Macdonald 1980b; Bakken 1993a; b; Hartley *et al.* 1994). Productivity is also reduced by incidence of mange (Pence & Windberg 1994) which is epidemic in nature and considered to be density-related. Fox productivity is therefore lowest where fox density is high or food supply is poor, i.e., when the population is near the environmental carrying capacity. Density-dependence in population growth is usually assumed in population dynamics models to account for these regulatory influences, and implies that by reducing density, culling will have a compensatory effect on productivity leading to an increase in population growth. Such increased productivity in culled populations has been indicated in some studies (Harris 1977; Cavallini & Santini 1996; Heydon & Reynolds 2000b) but not others (Devenish-Nelson *et al.* 2013).

Sexual maturity in foxes is reached at 9-10 months and most foxes will attempt breeding in their first adult year if a suitable territory is found (Lloyd 1980). Male foxes are seasonally fecund from November-March, with a peak in spermatogenesis from December-February; female foxes are receptive over a three-day period (Maurel, Lacroix & Boissin 1984; Macdonald & Reynolds 2004). The onset of breeding occurs in late-winter and is correlated with day length, starting earlier at more southerly latitudes (Lloyd & Englund 1973). The gestation period is 52 days, with most births in Britain occurring between mid-March and mid-April. One litter of cubs is produced per year with an average litter size of 4.5 cubs up to a maximum of 12 cubs (Lloyd 1980; Macdonald & Reynolds 2004). Of the sample of culled foxes from the FMS, the mean number of cubs born per pregnant female was 5.6 cubs (Chapter 2). Female foxes lactate for four weeks following the birth of cubs,

and the cubs are fully weaned at 6-8 weeks (Macdonald & Reynolds 2004). At about six weeks of age the cubs begin to emerge from the earths, initially only exploring the area around the entrance, but become more active away from the earth by eight weeks (Lloyd 1980). Cubs would therefore become vulnerable to lamping effort from eight weeks onwards.

Age-specific variation in the proportion of females breeding, with higher proportions of barren animals in first and oldest age classes, and variation in litter size, with smaller litters in first and oldest age classes, have been found in several studies (Englund 1970; Harris 1979; Kolb & Hewson 1980; Allen 1983; Cavallini & Santini 1996; McIlroy, Saunders & Hinds 2001); although Heydon & Reynolds (2000b) found no significant within-region variation in litter size when first-time breeders were compared to older age classes. Whatever the details, the assumption that productivity is similar across age classes must be made to enable reproduction to be modelled without age-structured data. Because there is also no sex-structure to the data, this can be achieved using a parameter for per capita birth rate. Assuming a 50:50 sex ratio and all females breeding, litter size estimates from the literature and the FMS data suggest fox per capita productivity is about 2.8 cubs per adult per year. Presence of non-breeding helper females within social groups would lower this value for the population, although such barren vixens are less common in populations subject to high levels of culling mortality (Lloyd 1980). As all of the fox populations surveyed by the FMS were subject to some degree of culling, presence of non-breeding females may not greatly bias the parameter estimation. Information on covariate factors, e.g., food availability, could improve inference on productivity; however, there is no such information within the FMS data other than broad-scale land classification.

3.1.2.3 Fox immigration

Due to the territorial structure of fox society, the fox population on an estate at any particular time is composed of resident foxes within a territory and itinerant foxes that are non-resident. Territories are relatively stable during the spring and summer, but come under pressure when foxes move across territorial boundaries for dispersal or for mating (Reynolds 2000). Dispersing foxes are usually juveniles leaving their natal range, with a variable

proportion of females and almost all males leaving (Macdonald & Voigt 1985). Dispersal occurs between August and March (Trehwella & Harris 1988), but mostly between October and January (Macdonald & Reynolds 2004). When a population is not subject to culling, immigration is predominantly a seasonal process determined by dispersal; however, culling causes major perturbation to the territorial structure to create local population sinks that are rapidly filled by replacement foxes (Reynolds, Goddard & Brockless 1993).

Most replacement foxes are thought to be itinerant foxes, especially during the dispersal period, but if territory-holders are culled then resident foxes occupying neighbouring territories will also move into the undefended area at any time of year (Reynolds 2000). Heterogeneity in local culling effort across the landscape means that a source population of foxes is usually close (Baker & Harris 2006). As fox movement is often across estate boundaries, immigration onto an estate following culling can therefore occur year-round, indeed, field evidence from gamekeepers suggests that immigration occurs throughout the summer in response to removal of adult foxes. In addition, movements of foxes may occur outside of the dispersal period if the earth of a family group is disturbed as the vixen will move the cubs to a different location that may be up to 1.5 km away (Lloyd 1980; Reynolds, Goddard & Brockless 1993). For estates where immigration rates are high, the constant replacement of culled foxes by immigrant foxes could explain why some populations remain stable or grow despite culling. Immigration is therefore a key process to include in models of local populations culled on restricted-areas.

The rate of replacement of culled foxes by immigration has not previously been studied, so any seasonality in this rate is unknown. Constant immigration throughout the year is therefore the basic assumption. Like productivity, immigration is a density-dependent process, because when fox density on an estate is high, e.g., due to ineffective or minimal culling, there will be less vacant territory space for immigrant foxes to move into. Immigration rate itself reflects neighbouring fox densities at some (regional or landscape) scale, so that if many estates in an area are culling foxes, density will be suppressed (Heydon & Reynolds 2000b) and immigration rates will therefore be lower.

3.1.3 Suitable modelling approaches

There is a vast literature on the modelling of harvested populations from fisheries and game management (e.g. Caughley 1977; Seber 1982; Roseberry & Woolf 1991; Hilborn & Walters 1992; Williams, Nichols & Conroy 2002). The population harvest and control processes share many similarities as the ability to exploit a population, either for harvest or control, depends on compensation (Hone 1994). Many of the harvest modelling approaches are therefore suited to culling data from pest control. Exploitation below a sustainable level provides a harvestable surplus, but exploitation above this level will reduce the population towards extinction. Population dynamics modelling is used to determine the exploitation level that gives the maximum sustainable surplus or yield (MSY). In harvested populations, management actions aim to keep the exploitation level near to MSY to both maintain a stable population and harvest the maximum surplus; in controlled populations, management actions aim to implement controls when the cost of damage by the pest exceeds the cost of control and then to reduce the pest population either until it is below an acceptable threshold level or it is eradicated (Hone 1994; Williams, Nichols & Conroy 2002).

A generic exploitation model can be used to describe a population that is being harvested or controlled (Hone 1994; Williams, Nichols & Conroy 2002):

$$N_{t+1} = N_t + f(N, t) - g(C) \quad \text{Eq. 3.1}$$

where $f(N, t)$ is a function describing non-linear growth processes (representing reproduction, mortality and migration) with respect to a deterministic population N between time t and $t+1$, and $g(C)$ is a function describing the harvest or control removals during the time period. Two approaches that use this generic model for estimating density are:

- 1) Population reconstruction, e.g., virtual population analysis, cohort analysis, or statistical age-at-harvest analysis (Downing 1980; Fryxell, Mercer & Gellately 1988; Hilborn & Walters 1992);
- 2) Depletion models, e.g., Leslie or DeLury estimators (Leslie & Davis 1939; DeLury 1947; Hilborn & Walters 1992).

Population reconstruction methods use growth functions that model the age classes and/or sexes separately, meaning the only suitable approach for modelling the age-aggregated FMS culling data (Chapter 2) is a depletion model. Depletion models are also designed to capture the within-year dynamics that are relevant to fox management decisions. However, classic Leslie or DeLury estimators are unsuitable for modelling local scale fox population dynamics where immigration is a key population process because they assume closed populations. This does not mean that alternative depletion model estimators are unsuitable for open populations, but means that simulation-estimation analysis must be conducted to determine sources of error and bias and to assess whether the available data contain sufficient information to reliably identify the deterministic parameters (Hilborn & Walters 1992).

Depletion models infer population density N_t by estimating how many additions into (by births or immigration) and removals out of (by mortality or emigration) the population must have occurred at each model time step. Together with known removals by culling, an observed pattern of change in a relative abundance index I_t , such as catch-per-unit-effort or sighting rate will be produced (Hilborn & Walters 1992). This is achieved by combining two submodels: a population dynamics submodel based upon Eq. 3.1 that predicts population density in time $t + 1$ given a parameter for initial population density N_0 and deterministic parameters for mortality, reproduction and immigration; and an observation submodel including a parameter that defines a proportional relationship between the population density and the abundance index. Parameter estimation is achieved by substituting the population submodel equations into the observation model equation to predict I_t values as a function of both the unknown depletion model parameters and the process and observation error variances. Bayesian estimation procedures such as Markov chain Monte Carlo (MCMC) may then be used to find the joint posterior parameter distribution of the parameters based on the fit of predicted I_t values to the observed time series of I_t from an estate.

Uncertainty in modelling population dynamics arises from process variation (environmental and demographic stochasticity), observation error, parameter uncertainty and structural uncertainty. A state-space model (SSM; Millar & Meyer 2000a; de Valpine & Hastings 2002; Buckland *et al.* 2007) allows the simultaneous estimation of deterministic

parameters, observation error, and process error in non-linear, non-normal ecological models with density-dependence (Bolker 2008; Lebreton & Gimenez 2013). When inference is made within a Bayesian framework, all of the above uncertainties can be quantified. In a Bayesian SSM, a process error submodel specifies the probability distributions associated with the population processes (i.e., mortality, reproduction and immigration); these combine to give rise to unobserved (latent) states which are subject to process variation. A corresponding observation error submodel defines the probability distribution of the observations, which are related to the states (Buckland *et al.* 2007). The process and observation error submodels correspond with the submodels in a depletion model. It therefore seems reasonable to consider both sources of error in a depletion model within a Bayesian state-space modelling framework; this has only recently been pursued in the fisheries literature (Robert *et al.* 2010; Ono, Punt & Rivot 2012) and is unexplored for terrestrial systems.

3.1.4 Determination of minimum data requirements

SSMs are notoriously data-hungry and insufficient information in the data can lead to model parameter identifiability problems, where more than one set of parameter values generates the same distribution of observations (Trenkel 2008). Such confounding can result in strong correlations in the joint posterior probability distribution and large parameter uncertainties (Schnute 1994; Buckland *et al.* 2007; Bolker 2008). The joint posterior distribution can have extremely high dimensionality as it includes deterministic parameters as well as latent states for each time step, which can lead to computational problems for long time series that show little variation. If correlations between parameters and states are high, convergence can also be prohibitively slow (Newman *et al.* 2009). Reducing the correlation between parameters in the posterior distribution, either by arbitrarily fixing parameters at some value or specifying an informative prior probability distribution for parameters can help, but neither of these options will work if the data are uninformative about several parameters.

For some FMS estates there are five-year time series of sighting rate data that contain frequent observations on a short time step with which to fit a model; however, for other estates there is much less data (Chapter 2). In fisheries, simulation-estimation analysis has been used to gain an understanding of what features make data informative or uninformative to enable identification of datasets for which models are likely to be biased or imprecise (Magnusson & Hilborn 2007; Robert *et al.* 2010). Three factors were hypothesised to contribute to the data information in a sighting rate time series: 1) the length of the time series, 2) between-year variation in the time series, and 3) missing data at some time steps. The simulation-estimation approach will be used here to determine which estates may have time series that are too short, vary too little, or otherwise contain insufficient information to estimate all parameters and fox density reliably.

3.1.5 Chapter aims

The aims of this Chapter were divided into two: 1) to formulate a generalised depletion model for a local scale fox population that incorporates the key processes of non-culling mortality, reproduction and immigration within a Bayesian state-space modelling framework that can be fitted using the type of data available; and 2) use simulation-estimation analysis to assess the performance of the model. The assessment will serve several purposes: i) to examine the effect of using of vague and informative prior probability distributions for deterministic parameters; ii) determine the minimum time series length and number of time steps that can have missing data before estimation becomes unreliable; and iii) determine variations in annual culling effort between-years that give more or less informative time series of data.

3.2 Methods

3.2.1 Data

FMS data (Chapter 2) only contain sex- and age-aggregated culling and sighting rate information, apart from the numbers of cubs killed at earths. The modelled fox population was defined as the ‘sightable’ population that gamekeepers can potentially sight whilst

lamping. This comprises adult foxes and cubs that become sightable once they are active away from the earth post-weaning. FMS data for some estates began on 1 January 1996 until 31 August 2000 and were recorded on a daily time step, giving a maximum of 1,705 observations. In a SSM, each latent state requires estimation and so modelling these data on a daily time step would result in a heavily over-parameterised model that would also take an unrealistic computation time to run. On average, gamekeepers went lamping on one night per week, so daily time steps were not necessary from a management perspective: decisions were seemingly made on at least a weekly time scale within an overall annual fox control strategy. It was therefore acceptable to aggregate the data into a longer time step.

Aggregating the data into a coarse time step, e.g. annual or quarterly time steps, was not considered an option, as it is the time-scale of within-year population dynamics that would allow immigration to be distinguished from reproduction. Estimation procedures for depletion models rely on the fact that removing animals from a population has a noticeable effect on an observed abundance index such as sightings per unit effort. Loss of information on the effect removals had on the sighting rate also becomes a problem with aggregation into longer time steps, which in an open population depletion model makes it more difficult to determine immigration. The time scale on which process errors occur was also a consideration. Environmental processes affecting fox numbers, such as bad weather over winter or during the breeding season, are annual or at most seasonal. By contrast, the demographic processes that affect fox populations, such as immigration, operate on much shorter time scales. Intensive radio-tracking data suggests that replacement of territory-holding foxes removed by culling can occur within two weeks (unpubl. data, GWCT), but movement can occur over even shorter time scales, e.g. if a disturbed vixen moves with a litter of weaned cubs. Such variable numbers of immigrant foxes can cause spikes in sighting rate that are difficult to model using a mean rate, leading to large process errors. That foxes are present in relatively small numbers on an estate amplifies the problem, as the density can change by large proportions from one time step to the next. To balance all the above factors, weekly or two-weekly aggregation seemed suitable. From initial model runs, differences between the results from a weekly time-step model and those from a two-weekly

time step model were found to be within 5%. For this simulation-estimation study, data were generated using an operating model defined on a weekly time step.

3.2.2 Timing of fox breeding events

Cubs become vulnerable to lamping at a particular age depending upon when they are weaned. To account for cub recruitment into the sightable fox population, the time at which this occurs must be defined. While most cubs are born in late March, making the assumption that all cubs are weaned in one week and become sightable at the same time was considered too rigid. A more realistic approach would be to specify a weaned week distribution that incorporated variation around the mean entry week to allow for some early or late litters across an estate.

The first step in obtaining this distribution was to use data from fox populations in SE England and Wales describing the probable conception dates of female foxes killed during pregnancy (Lloyd 1980). These data were summarised by taking the mean date and percentage of paired sampling points ($n=5$) on the ascending limb of the curves, i.e. the percentage of females that had conceived over time across both populations). Next, assuming that these mean data points followed a logistic distribution, the ‘fitdistr’ function from the MASS package (Venables & Ripley 2002) in the R statistical software (R Core Team 2013) was used to estimate the maximum likelihood values of the parameters describing the cumulative distribution function of the logistic distribution. This cumulative distribution was taken to describe the distribution of conception events in the female fox population over time.

Given the distribution of conception events it was trivial to project this forward in time, first to a distribution of cub births by assuming a gestation period of 52 days, and then to a distribution of cub weaning by assuming that all cubs were weaned by eight weeks old (56 days). As expected, the mean of the distribution of births was in late March. This distribution was then used to calculate the proportion of cubs weaned on a given day and thereby vulnerable to lamping in the sightable population. These proportions were then

aggregated into a weekly time step w_t for use in the model, with w_t defined as the proportion of weaned cubs entering the sightable population in week t (the values of w_t sum to 1).

3.2.3 Process model for population dynamics

Fox populations on FMS estates were modelled in units of density so that parameter estimates would be comparable across estates. The proposed open-population depletion model assumes that on each estate the sightable fox density, N_t , in week t depends on the density at week $t - 1$, the cumulative cull between $t - 1$ and t , non-culling mortality, cub recruitment, and immigration. The model is initialised by N_0 , the initial fox density in the first week of the sighting rate time series, which depending upon the estate was either 1 January, 1 March or 1 September. Non-culling mortality was modelled as an instantaneous weekly rate M . This instantaneous rate is equal to the weekly probability of survival for the foxes which remain on the estate following the removals of culled foxes each week. For reasons detailed above, M was assumed to be constant over time.

The recruitment of weaned cubs and immigration into the sightable fox population each week were assumed to be density-dependent processes. Density-dependence was modelled using simple logistic terms based on the notion of a carrying capacity, K , describing the pre-breeding fox density at which recruitment and immigration become zero through density-dependent feedback. K is assumed to be determined by resource availability, and thus specific to each estate. Cub recruitment was modelled using a *per capita* birth rate parameter, r , representing the maximum number of cubs that would be recruited annually if the population was at low density relative to K . Cubs culled at earths were assumed to be of pre-weaning age; by adding cubs into the population post-weaning following the w_t schedule non-culling mortality of pre-weaned cubs is implicitly incorporated in r . This is therefore when any density-dependent effects on cub recruitment will occur. Net immigration was modelled using a parameter for immigration rate per km^2 , v , representing the maximum weekly rate of replacement if the population was at low density. If fox density is at carrying capacity, no cubs are recruited and there is no immigration into the population. Similar approaches to modelling density-dependence in seasonal reproduction and/or immigration in

fox populations have been used in estimation models for the spread of rabies (Bacon 1985; Smith 1985) and in a simulation model examining control by contraceptive or poison baits (McLeod & Saunders 2014); but this is the first time that both reproduction and immigration have been employed in the same estimation model. K , v and r were also assumed to be constant over time.

Based upon the generic exploitation model (Eq. 3.1) and conditioning it on the total cull, fox density in week t was assumed to follow the state equations below:

$$N_1 = N_0 e^{\varepsilon_1 - (\sigma_p^2/2)} \quad \text{Eq. 3.2}$$

$$N_t = [N_{t-1} e^{-M} + v(1 - N_{t-1}/K) + J_{t-1} - L_{t-1} - S_{t-1}] e^{\varepsilon_t - (\sigma_p^2/2)} \quad \text{Eq. 3.3}$$

$$J_t = w_t r N_t (1 - N_t/K) - C_t \quad \text{Eq. 3.4}$$

where J_t is the weaned cubs recruiting in each week t , L_t is the cull from lamping, S_t is the cull from other methods (of which most are from snaring), and C_t is the cull cubs at earths, which are assumed to be pre-weaned cubs. For numerical stability, N_t was constrained within the model to be non-negative (≥ 0.001 fox km⁻²). Process errors were assumed to be independent and identically distributed (iid) multiplicative lognormal (Halley & Inchausti 2002), obtained by randomly sampling ε_t from a standard normal distribution that has a standard deviation σ_p :

$$\varepsilon_t \sim N(0, \sigma_p) \quad \text{Eq. 3.5}$$

The lognormal bias correction factor ($-\sigma_p^2/2$) was applied to the state equation so that it reflected expected N_t rather than median N_t .

All observed cull numbers were converted to density of foxes killed per km² using the estate area. To account for cubs being killed at earths in any week from birth until weaning age rather than just in the week they recruit as implied in Eq. 3.3, all cubs culled at earths in year y were summed and re-distributed into each recruitment week t following the w_t schedule to calculate normalised values for C_t within each year:

$$C_{t,y} = w_t \sum_{y=1996}^{2000} C_{t,y}^{obs} \quad \text{Eq. 3.6}$$

This was necessary to ensure that cubs culled at earths within each year were not removed from the model before they had been produced in a given week t .

3.2.4 Observation model for sighting data

For estimation using the proposed model, a linear relationship with zero intercept was assumed between observed fox sighting rate, I_t , and the unobserved fox density, N_t , with a scaling parameter that is constant over time (Caughley 1977; Roseberry & Woolf 1991; Hilborn & Walters 1992). For a full discussion of this assumption, see Chapter 6. Across FMS estates, the mean number of foxes sighted per week was 2.52 fox wk⁻¹ (± 0.05 s.e., $n=4067$ weeks). Given such low numbers, it is more appropriate to model the discrete number of sightings rather than the continuous sighting rate. In addition, there were a large number of weeks when no foxes were sighted. Zero sightings can occur when there are either no foxes available to see or there is no lamping effort in a given week. Fitting the model to sighting rate would mean that both of these events would be represented by a zero, therefore losing information on fox density from zero sighting events that occurred under variable levels of weekly lamping effort. Instead of fitting to sighting rate, the model was fitted to the observed number of fox sightings, Y_t , with the observation errors assumed to be Poisson distributed:

$$Y_t \sim \text{Pois}(dE_t N_t) \quad \text{Eq. 3.7}$$

where E_t is the number of lamping hours and d is a scaling parameter with units km² hr⁻¹, which is assumed to be constant over time. Given that sightings might be aggregated due to social heterogeneity among individuals, and that there were many weeks with zero sightings due to lack of lamping effort, alternative distributions that allowed for over-dispersion and zero-inflation were considered. The Poisson distribution was chosen following exploratory analysis which suggested that the best fit to the sighting data on the majority of FMS estates

was achieved by the Poisson distribution, rather than the negative binomial, zero-inflated Poisson, or zero-inflated negative binomial.

In a classic depletion model with no recruitment, immigration or process errors, the state equation can be rearranged and substituted into an observation model such that N_0 and d can be estimated by linearly regressing sighting rate on cumulative cull (Hilborn & Walters 1992). Estimation of the proposed depletion model in a Bayesian state-space modelling framework with both process and observation errors is complicated by two main difficulties: 1) the inclusion of additional terms for cub recruitment and immigration rule out the simple rearrangement of the state equation and therefore use of simple linear models, and 2) process errors are multiplicative and therefore propagate through time (Robert *et al.* 2010). Bayesian approaches to parameter estimation, such as Markov chain Monte Carlo (MCMC) integration, can fortunately overcome these difficulties to sample directly from the joint posterior distribution of the unknown parameters and latent states in the model.

3.2.5 Prior probability distributions for parameters

The estimated parameters in the model were N_0 , K , v , r , M , d and σ_p . For the initial part of the simulation-estimation analysis, vague priors were set for all parameters as defined in Table 7.3. These all took uniform distributions with large bounds, where the upper bounds took values that were the maximum considered biologically possible. The fox density in an urban population from Bristol was used as the upper value for both N_0 and K (13.9 foxes/km², Soulsbury *et al.* 2007). The Bristol population was at this density for several years prior to a period when the density tripled and an epizootic of mange occurred, so it was considered to be a ‘healthy’ urban density representing the maximum a rural population could reach if food availability in rural areas was increased to urban levels. The upper value for v represented an annual immigration rate of >50 foxes/km², which was considered plausible only in urban areas. The upper value for r was based upon a reported maximum litter size of 12 cubs per female (Macdonald & Reynolds 2004) with the added assumption that these were from a fox population with a 50:50 sex ratio. The upper value for M translated to an annual non-culling mortality rate of >99%. This is a very high value but in

theory it is biologically plausible if immigration was extremely high. The upper value chosen for d would require a gamekeeper to search the estate area at a rate of 10 km^2 per hr which would not be easy even if driving on well-maintained roads. The upper value of 0.5 for σ_p meant that a deterministic prediction of N_t equal to 2 foxes/km^2 could approximately halve or double from one week to the next due to process error variation.

The relative influence of priors and the data depends on their relative precisions ($1/\text{variance}$, Kuhnert, Martin & Griffiths 2010). Informative priors convey some prior knowledge about a parameter and consequently have higher precision relative to vague priors. In situations where the data are uninformative about key model parameters the use of informative priors, provided they are constructed without bias, can be particularly useful at determining reasonable parameter bounds and thereby help to reduce estimation uncertainty (McAllister *et al.* 1994; Hilborn & Liermann 1998; Kuhnert, Martin & Griffiths 2010). Informative priors for v , r , M and d were therefore explored in subsequent parts of the simulation-estimation analysis. These were parameters for which other sources of data were available that could be used to establish informative priors for them. These analyses are detailed in later Chapters in this thesis, with the CV values used here taken from them.

3.2.6 Simulation-estimation analysis

Performance of the estimation method using the proposed depletion model within a Bayesian state-space modelling framework was evaluated using simulated data. The simulation-estimation analysis consisted of several separate steps which are detailed below.

3.2.6.1 Generation of lamping effort schedules

To examine the performance of the estimation model, the simulation-estimation analysis required that alternative lamping effort schedules were generated. Lamping effort data were generated on a weekly time step with a reference time series length based upon the length of the longest FMS time series. This covered 243 weeks between 1 January 1996 and 31 August 2000, and five breeding seasons. The expected number of hours of lamping in each week was obtained by scaling the mean weekly effort observed across estates and years

($1.68 \text{ hr week}^{-1} = 87 \text{ hr yr}^{-1}$) by the proportional effort in each week during the year. This gave realistic seasonal variation in lamping effort, with less effort in summer and mid-winter and more effort in the spring and post-harvest (Fig. 2.3a). To allow for between-week variation in effort within this annual pattern, but ensure that expected annual effort remained constant, E_t values were generated as Poisson-distributed random variables with expectation equal to the scaled mean weekly effort values.

The simulation-estimation analysis was split into three parts: 1) choice of vague or informative priors, 2) different time series length, and 3) different variability in annual culling effort between-years. For parts one and three of the analysis, the reference five-year E_t time series were obtained by multiplying the scaled mean weekly effort values in each year by the annual multiplier vector (S1, Table 3.2). For part two, the number of breeding seasons covered by the time series was varied to give time series that were two, three, four and five years long. The scaled mean weekly effort values were the same in each year. For part three, variable annual effort schedules were compared to the reference schedule (S1). To allow a comparison of the results from different effort schedules, the total effort over the five-year period was kept the same in each schedule, but the effort used in each year was varied. The same seasonal variation in effort was maintained. The alternative effort schedules explored were considered achievable in the field based upon the range of data in the FMS. The FMS data suggested that on most estates the effort per unit area showed a year-on-year decrease over the duration of the study, so one alternative schedule showed decreasing annual culling effort over time (S2, Table 3.2). The complement to the decreasing schedule was one where annual culling effort increased over time (S3). Countless variations exist, but were limited to three variants which explored having limited and excessive effort years with abrupt changes to mimic a gamekeeper putting a lot of effort in for one year but taking a rest in the years either side (S4-S6). The numbers of weeks' without any lamping effort were summarised.

3.2.6.2 Simulation of data

The known ('true') sightable fox population dynamics were simulated using an operating model with known parameters, process errors, and observation errors (McAllister

et al. 1999; Rademeyer, Plagányi & Butterworth 2007). The operating model contained Eq. 3.3 - Eq. 7.5, which were used to simulate N_t time series using parameter values defined in Table 3.3.

The operating model also contained a set of equations to simulate the culling data needed to calculate N_t and numbers of fox sightings for fitting the model. Weekly cull data were simulated given the assumption that as sightable foxes, they were active away from the earth and vulnerable to both lamping and snaring culling risks. The order by which L_t or S_t occurred in a given week was randomised by simulating a Bernoulli random variable, h_t , that took a value of zero if lamping occurred first, or a value of one if snaring occurred first. Y_t in a given week were then simulated from N_t as a Poisson-distributed random variable given a weekly lamping effort schedule E_t :

$$Y_t \sim \begin{cases} Pois(dE_t N_t) & h_t = 0 \\ Pois(dE_t [N_t - S_t]) & h_t = 1 \end{cases} \quad \text{Eq. 3.8}$$

where d is the scaling parameter. L_t was then calculated as:

$$L_t = p_k Y_t / A \quad \text{Eq. 3.9}$$

where p_k is the probability of a sighted fox being killed (lamping success) and A is the estate area. The mean observed value of p_k from the FMS data was 0.30, but there was large variation in this value reflecting times when gamekeepers were unable to shoot any of the foxes sighted, and others when all foxes sighted were shot. This led to the observed distribution of p_k being U-shaped, as most values were either at 0 or 1. To model variation in the probability of lamping success per week, values for p_k were randomly generated from a distribution based upon the beta-binomial. The beta-binomial distribution is a binomial distribution with parameters for the number of trials and probability of success, but whose probability of success is not a constant but it is generated from a beta distribution. This allows U-shaped distributions, but without modification the generated numbers range from zero to the number of trials. To constrain the generated numbers to the $[0, 1]$ interval required, it was necessary to divide them by the number of trials (set equal to 100 here). Numbers were generated using the `rbetabinom` function from the R package VGAM (Yee

2010)(Yee 2010) with values of 0.3 and 0.75 for the ‘prob’ and ‘rho’ arguments, respectively. S_t was simulated as:

$$S_t = \begin{cases} p_s(N_t - L_t) & h_t = 0 \\ p_s N_t & h_t = 1 \end{cases} \quad \text{Eq. 3.10}$$

where p_s is the probability of snaring success per fox per week, which was assumed to be constant over time. C_t was assumed to be removed immediately prior to recruitment of cubs into N_t in week t :

$$C_t = p_c w_t r N_t (1 - N_t/K) \quad \text{Eq. 3.11}$$

where p_c is the probability of a cub being killed at an earth, which was assumed to be constant over time. Data from 39 earths suggest that nearly all (88%) of cubs seen at earths are killed (Reynolds 2000). If the assumption is made that once an earth has been found all cubs are killed, e.g. by using terriers to bolt them above ground to waiting shotguns, this probability will equal the probability of locating an earth on an estate.

A number of initial simulation runs were used to check that the true parameter values (Table 3.3) and lamping effort schedules simulated plausible culling data and fox density time series that were within the range of known regional spring and autumn fox densities (Heydon, Reynolds & Short 2000). Particular attention was given to the value of σ_p such that reasonable week-to-week variation in fox density due to process error was produced (range of variation in N_t was by a factor of 0.7-1.5). For each lamping effort schedule within each part of the simulation-estimation analysis, the operating model used to simulate 20 datasets to allow the performance of the estimation method to be evaluated.

The base case true parameter values for v , r , M and d in Table 3.3 were close to the informative prior medians for these parameters. The sensitivity of the estimation results to the true parameter values used to simulate N_t was examined by simulating two alternative sets of 20 datasets. The true values used in these alternative simulations were: 1) 0.5 times the base case values in Table 2.3 for N_0 , v , r and M , and 1.5 times the base case value for d , giving fox densities relative to K that were lower than those using the base case set of true

values; and 2) 1.5 times the base case values for N_0 , v , r and M , and 0.5 times the base case value for d , giving fox densities relative to K that were higher than those using the base set of true values.

3.2.6.3 Bayesian estimation

The simulated time series of lamping effort, numbers of fox sightings and cull numbers were considered as data and Bayesian estimation was performed on each dataset within the state-space modelling framework to estimate the true fox density and parameter values. The estimation model used was the same as the operating model used to simulate the data, meaning that any differences between simulated and estimated values were due to the performance of the estimation method and not to mis-specification of the model. Samples from the joint posterior probability distribution of the unknown parameters and latent states $p(N_0, K, v, r, M, d, \sigma_p, N_t | \text{data})$ were simulated by MCMC integration using WinBUGS 1.4 (Spiegelhalter *et al.* 2007) implemented from within R using the R2WinBUGS package (Sturtz, Ligges & Gelman 2005).

Use of the state equations in Eq. 3.2 - Eq. 3.4 resulted in slow mixing of the Markov chains over the support of the joint posterior due to correlation between the latent states and carrying capacity. This problem was reduced by reparameterising the states, expressing fox density as a proportion of carrying capacity ($P_t = N_t / K$; Meyer & Millar 1999a; Millar & Meyer 2000b). The state equations used in the model were therefore rewritten as:

$$P_1 = (N_0/K)e^{\varepsilon_1 - (\sigma_p^2/2)} \quad \text{Eq. 3.12}$$

$$P_t = [P_{t-1}e^{-M} + v/K(1 - P_{t-1}) + G_{t-1} - L_{t-1}/K - S_{t-1}/K]e^{\varepsilon_t - (\sigma_p^2/2)} \quad \text{Eq. 3.13}$$

$$G_t = w_t r P_t (1 - P_t) - C_t/K \quad \text{Eq. 3.14}$$

where G_t is the reparameterisation of J_t . The observation equation was rewritten as:

$$Y_t \sim \text{Pois}(dE_t P_t K) \quad \text{Eq. 3.15}$$

For comparison to true fox density, the marginal posterior estimates of N_t were obtained as the product of P_t and K .

Each simulation-estimation run used two independent MCMC chains with initial values chosen randomly from the joint prior. In the Markov chains, some parameters showed strong autocorrelation. To reduce the problem only 1 in 100 iterations were recorded after the first 100,000 iterations were removed as the burn-in. Inferences were then derived from a sample of 20,000 iterations from two chains of 10,000 iterations. Convergence of the Markov chains to the posterior distribution was diagnosed using the R coda package (Plummer *et al.* 2006). Gelman-Rubin convergence statistics (Gelman *et al.* 2004) were <1.1 for all parameters and Geweke's Z-scores (Geweke 1992) did not fall within the extreme tails of a standard normal distribution, suggesting that the chains had fully converged. In total there were 12 lamping effort schedules to evaluate within the three parts of the simulation-estimation analysis, which meant 240 runs were needed. Initial runs were slow and took up to 12 hours computation time, so parallel computing was used to increase estimation speed by 50% using the R snowfall package (Knaus 2013).

3.2.6.4 Measurement of estimation bias

The performance of the estimation method was evaluated by determining how well the marginal posterior probability distribution of each parameter and latent state estimated the true value used in the simulation of each dataset. For each parameter θ this was measured using the median of the marginal posterior to compare to the true value and summarised by calculation of the percent relative bias (PRB):

$$\text{PRB} = 100[(\text{estimated } \theta - \text{simulated } \theta)/\text{simulated } \theta] \quad \text{Eq. 3.16}$$

Bias plots were used to summarise the PRB for $[N_0, K, v, r, M, d, \sigma_p]$ across the 20 simulated datasets. The marginal posteriors were also evaluated visually against the true parameter values to examine the precision of parameter estimates.

The PRB in each latent state estimate was similarly calculated by comparing the median of the marginal posterior in each week to the true fox density. The mean of these

density PRB values was then calculated across the length of the time series and summarised across the 20 simulated datasets using a bias plots. The median of the marginal posterior for each latent state was also compared visually to the true fox density in each week to examine the fit of the model along the time series.

3.3 Results

3.3.1 Timing of fox breeding events

The estimated distribution of conception events from the data in Lloyd (1980) is shown in Figure 3.1, together with the projected distributions of births and weaned cubs. These projected distributions are supported by the weekly FMS data pooled across estates on the number of cubs killed at breeding earths. This shows that very few cubs were killed before the start of the projected distribution of births and that only a small proportion of cubs were killed at earths following the end of the projected distribution of weaned cubs.

3.3.2 Influence of prior distribution specification

Estimation models using either vague or informative priors were generally able to recover the weekly N_t trajectory from simulated datasets reliably as the posterior medians of N_t track the true fox density very well (Figure 3.2). The use of vague priors resulted in some overestimation of N_t for certain datasets especially during the summer. Informative priors led to narrower 80% credible intervals. Examination of the mean bias in posterior median N_t estimates across the length of the time series showed that estimation bias of N_t using vague priors was generally low (median PRB <10%), with only a slight bias reduction achieved from using informative priors (median PRB 3%; Figure 3.3).

The influence of informative priors was more apparent when examining the bias in parameter estimates, as identifiability problems when using vague priors resulted in large estimation bias for some parameters. M was grossly overestimated, with median PRB almost 200% larger than the true value (Figure 3.3). However, it should be noted that this bias only refers to the central tendency of the marginal posterior, and uncertainty in the estimates of M from model using vague priors was also large (Figure 3.4). Indeed, the true value of M was

found within the 80% credible interval (CI) of the marginal posterior for all but one dataset despite the posterior median being an overestimate for all. Given the poor estimates of M , it was expected that M would be highly confounded with the other parameters; however, posterior correlations between any of the parameters were not strong (correlation coefficient > 0.7). There were moderate posterior correlations (0.4-0.7) between M and ν (positive) and between M and σ_p (positive) in the results from a number of the datasets, but the coefficients between M and other parameters were all < 0.4 , reflecting weak posterior correlation. The use of an informative prior on M resulted in much smaller bias in estimates of M (Figure 3.3) and also had the effect of removing the correlation between M and ν or σ_p .

The vague prior model resulted in precise estimates of both ν and d (Figure 3.4), but ν was precisely overestimated while d was minimally-biased (Figure 3.3). These results were improved with the use of an informative prior on ν , which resulted in minimally-biased posterior medians and 80% CIs which encompassed the true value of ν for all datasets. Both N_0 and K also tended to be overestimated when using the vague prior model, with median PRB for both around 40%. This was improved to 15% when informative priors were used on the other parameters. However, similar to M , the large uncertainty in estimates of K and to a lesser extent of N_0 , meant that the true value of N_0 and K was found within the 80% CI for all datasets. The true value of r was found within the 80% CI of the marginal posterior under both models, but although the small positive bias was similar in both, the vague prior model resulted in some median values for $r > 50\%$ different from true values. These extreme values were not found when an informative prior on r was used. The choice of prior on the estimation of σ_p had little effect. Although the bias in σ_p was not large using either vague or informative priors, there were some datasets where the true value was outside the 80% CI of the marginal posterior when either type of prior was used.

Aside from moderate positive posterior correlations between ν and M from most datasets, there was moderate negative posterior correlation between r and K in the results from roughly half of them. There was also some moderate negative correlation between ν and r in the results from a couple of datasets, indicating features which made it difficult for the model to determine whether immigration was large and cub production small, or *vice*

versa. The most noticeable feature of these particular simulations was the higher number of weeks in which there was zero lamping effort during the May-June period when weaned cubs were recruited into the population.

The informative prior model resulted in an improvement in both the estimates of the parameters and the latent states. In absence of knowledge about true parameter values, the sensitivity to the choice of prior would rely upon model selection criterion, such as the Deviance Information Criterion (DIC). The model using informative priors was the ‘best’ choice as determined by DIC in 85% of datasets, with a mean difference of 3.2. Though this difference is only weak evidence in favour of this choice, the largest differences in DIC were for those simulated datasets where the posterior median fox density showed the largest departure from the true values and so where the choice is most important.

3.3.3 Effect of time series length

Time series of ≤ 2 years gave results with a median PRB in mean weekly fox density estimates of close to zero, but there were some datasets which resulted in extremely biased results where mean weekly fox density was overestimated by almost 100% (Figure 3.5). The results from longer time series did not contain such biased estimates. For time series of 3 years and longer the effect of extra time in reducing bias in fox density estimates was small, because in general the weekly trajectories of fox density were recovered reliably.

The length of time series did have a large effect on the ability to reliably estimate certain parameters, indicating identifiability issues when fewer time steps were present in the data. In particular, time series of ≤ 2 years resulted in large overestimates of K and σ_p , with median PRB of 65% and 30%, respectively (Figure 3.5a). Examination of the marginal posteriors for these parameters showed that the bias in K resulted from minimal posterior updates to the prior, with the bias reflecting where the true value for K (4.0 fox km^{-2}) was in relation to the median of the prior (6.9 fox km^{-2}). For σ_p the marginal posteriors were hugely variable, which unlike for K meant that the true value was often outside of the 80% CI for σ_p . These biases were reduced as time series became longer (Figure 3.5b-d). Bias in v , r , M and d was minimal (Figure 3.5), but in the shorter time series this was largely due to the

influence of the informative priors, which, especially for r and M , received minimal posterior updates.

There were no strong posterior correlations between any of the parameters estimated using datasets of any length, and the use of informative priors meant that even with short time series, moderate posterior correlations were limited to one or two parameter pairs per dataset. Across the results from all datasets, the mean number of parameter pairs showing moderate correlation decreased as the time series became longer, from 1.3 (range 0-3) in 2 year time series to 0.9 (range 0-1) in 5 year time series. In shorter time series, posterior correlation was most commonly found between N_0 and σ_p (positive) and between v and r (negative); while in longer time series negative correlation between r and K was more common.

3.3.4 Effect of effort variability

The effect of varying the annual effort on parameter bias is seen by comparing the reference schedule (S1) to the alternative lamping effort schedules (Figure 3.6). The differences in parameter estimate bias between the alternatives was not as large as expected, the model performing equally well with the constant effort reference schedule as with alternative schedules which showed large effort variations. However, r was better estimated when there were large year-to-year variations in lamping effort (S4-S6, Figure 3.6). Across both N_t and all parameters, performance (determined by total median PRB) was slightly better from the schedule in which effort varied the greatest from year-to-year (S6, Figure 3.6). Results were also affected when the periods of high and low effort occurred, the greatest bias in estimates of N_0 arising when effort was minimal in the first two years (S5, Figure 3.6). Estimate precision followed a similar pattern to estimate bias, with larger CV for N_0 and K , as well as M (Table 3.4). The least biased parameters were v and d , these were also the most precisely estimated. There was little difference between lamping effort schedules on the precision of v , r , d and σ_p . Large variations in lamping effort (S4-S6) resulted in improved precision for K and M . For N_0 , the CV was only improved slightly under S4 and S6, but was considerably higher under S5.

The increasing and decreasing effort schedules (S2, S3) both resulted in overestimation of mean weekly fox density, but the median PRB remained below 8% (Figure 3.6). However, there were large differences in the reliability of weekly fox density estimates between the different effort schedules. Compared to the reference schedule (Figure 3.7a) the departure of estimated density from simulated density was much greater in those years with <50% of the mean effort level, while N_t estimates in years during which the effort level was increased were estimated with less error (Figure 3.7b-f). The differences were clearly related to the number of weeks with lamping effort. Using the mean weekly effort of 1.68 hr, the expected number of weeks with lamping effort per year was 42 weeks per year. At one-half of this effort level, this decreased to 30 weeks, while at one-tenth this level of effort (the lowest annual amount explored here), it was expected that there would only be 8 weeks with sighting rate information. Years in which there were less than 8 weeks with lamping effort resulted in the worst weekly fox density estimates (Figure 3.7d-f). Increasing the level of effort by 50% above the mean meant that only 4 weeks per year were expected to be without lamping effort. This corresponded to much improved density estimates.

3.3.5 Sensitivity to true parameter values

The sensitivity of results to the values used for N_0 , v , r , M and d to simulate the weekly N_t trajectories showed that when compared to the base case set of true values, the use of true values that were low or high compared to the informative prior medians did affect the estimations. However, the effect on the ability of the estimation model to recover the true fox density was small as the posterior medians of N_t tracked the true fox density well when N_t relative to K was either lower (Figure 3.8) or higher (Figure 3.9) than the base case. Across the length of the time series, the mean percent relative bias in posterior median N_t from using lower or higher true values was 9% and 11%, respectively, compared to 3% with the base case values.

Some parameter estimates were more sensitive to the alternative sets of true values within an informative prior estimation model. The effects were dependent upon whether the values were larger or smaller. In the low population case, the worst estimates were of M ,

which was consistently overestimated relative to the lower true value in this case. The median PRB was 119% and true values were below the 80% CI of the marginal posteriors for four datasets (Figure 3.10a, Table 3.5). r was also consistently overestimated, although this was expected as the lower value in this case ($1.4 \text{ cub fox}^{-1}\text{yr}^{-1}$) was only in the second percentile of the prior distribution and was thus extreme. The median PRB was 47% and true values were below the 80% CI for six datasets (Figure 3.10a, Table 3.5). In contrast, K was better estimated than when the base case values were used and median PRB indicated that estimates of K were minimally-biased in this case (Figure 3.10a, Table 3.5). While d was minimally-biased when base case values were used, d was underestimated relative to the higher true value in this case although median estimates were on average within 12% of true values (Figure 3.10a, Table 3.5). The median estimates for other parameters were all within 5% of the base case (Figure 3.10a, Table 3.5). The marginal posteriors for σ_p were overestimated on average by 9%, but this was not consistent between datasets and for many the true values were close to either the upper or lower 80% CI (two were above, one below). Apart from r and M , the true values for the other parameters were within the 80% CI for nearly all (>85%) datasets.

In the high population case, r and M were typically underestimated relative to their higher true values, although there was more posterior updating for these parameters than seen in the low population case (Figure 3.10b). This was reflected by median PRB being only –9% and –16%, respectively, and the true values of r being outside the 80% CI of the marginal posteriors for only two datasets. True values for M were within all 80% CIs. This case resulted in poorer estimates of K as median estimates were on average 38% higher than the true value, but the true value for K was outside of the 80% CI of the marginal posterior for only two datasets. The median estimates for other parameters were on average all within 5% of the base case, with true values within the 80% CI for nearly all datasets. Posterior correlations in the results using the alternative sets of true values were similar to those observed under the base case set of values when using informative priors (see 3.3.2).

3.4 Discussion

3.4.1 Choice of priors

This Chapter describes a novel approach to estimating the density and demographic parameters of a fox population in the context of restricted-area culling, using data that can be collected in the course of the culling process. An SSM of fox population dynamics was formulated which builds on an open-population depletion model structure to explicitly incorporate non-culling mortality and both density-dependent cub recruitment and immigration. Using the model to simulate realistic non-age-structured fox populations and then using the same model within a Bayesian estimation framework with informative priors derived from the literature resulted in reliable estimates of N_t , with parameter estimates also reliable for most simulated datasets. In comparison, the model performed worse at estimating both N_t and the parameters when given vague priors, and this was also reflected by larger DIC values. Vague prior estimates of N_t were generally similar to those from the informative prior model but with wider credible intervals. However, with some datasets use of the vague prior model resulted in overestimation of N_t during the summer months. The estimates of r from these datasets were notable for being positively biased. These datasets also had by chance a lower number of weeks in which there was lamping effort during the summer. As a result, it appears insufficient information in the data during the summer months leads to overestimation of cub recruitment without an informative prior on r , and consequently N_t is overestimated for this period.

Even with longer time series of data, the vague prior model resulted in poor estimates of some parameters, in particular the estimates of M and K . This suggests that despite reasonably reliable N_t estimates the model had identifiability problems when vague priors were used. Given this, it was surprising that none of the pairwise posterior correlations between parameter combinations were strong, which would indicate confounding (Trenkel 2008). A model that is not identifiable has redundant parameters; this may either be intrinsic redundancy, which is a model property, or extrinsic redundancy, meaning not all model parameters are identifiable for a specific dataset (Gimenez *et al.* 2004; Trenkel 2008). This

model contains additional parameters compared to a classic depletion model in order to account for density-dependent cub recruitment and immigration; hence the risk of non-identifiability is increased. During the initial stages of model formulation, maximum likelihood was used to determine whether it was possible to estimate the parameters of an observation-error only model, and most simulated datasets resulted in reasonable estimates and positive-definite Hessian matrices (Gimenez *et al.* 2004). The non-identifiability was therefore determined to be due to extrinsic redundancy as it was an issue only for some datasets; use of informative priors overcame this problem.

SSMs with density-dependence are known to have extrinsic redundancy problems (Kéry & Schaub 2012) as the parameter determining the strength of density-dependence often proves difficult to estimate, especially when observation errors are large (Knappe 2008). As the CV of observation error was about 20 times larger than the CV of the process error (1.37:0.07) this partly explains why estimates of K were biased under both vague and informative priors. The results also found that bias in K was higher from those simulated populations where N_t spent little time near to K . Culled fox populations can be assumed to be at low densities relative to carrying capacity due to the continual removal of foxes, and these populations were simulated such that N_t would spend most time below 50% of K . As a consequence, estimates of K were uncertain as N_t did not spend long enough around K for density-dependent effects on cub recruitment and immigration to be clearly observed. Although an informative prior was not available for K , the use of informative priors on the other model parameters resulted in improved estimation of K due to the joint posterior space being constrained. Uncertainty in K would be reduced if either covariate data that would influence K , such as food availability, were available, or if an informative prior could be established. The estimates of N_t were not greatly affected by the uncertainty in K because when N_t is considerably smaller than K , the dynamics of the fox population are fairly insensitive to the value of K (Figure 3.11). As shown by these simulations, the value of K only becomes important if N_0 is relatively large. When N_0 is <50% of K there is little difference in N_t trajectories values of K between 4 and 25 fox/km². This property helps to explain the difficulty in estimating K from culled populations.

For estimation of M using the vague prior model, the addition of process error within the SSM framework made the non-identifiability problem worse as confounding between M and σ_p resulted in moderate positive posterior correlation between these parameters. Depletion model applications in the fisheries literature often choose to fix M at some value to remove such identifiability problems (McAllister *et al.* 2004; Robert *et al.* 2010). Given the lack of posterior updating of M , with the posteriors closely reflecting the prior, there is an argument that M should be fixed here as it appears to be only weakly identifiable. However, fixing parameter values does not admit any parameter uncertainty, so use of an informative prior to both reduce the identifiability problems and incorporate parameter uncertainty is preferable (Hilborn & Liermann 1998). Besides σ_p , M was also positively correlated with ν when using vague priors. Uncertainty in estimates of ν was low, so it would appear that the small positive bias in ν estimates arose from the positive posterior correlation with M . The use of the informative prior model removed the moderate posterior correlations which existed with M under the vague prior model, and accordingly the use of informative priors resulted in an overall reduction in bias in the other parameters when the base case set of true values was used.

Further evidence of the weak identifiability of M in this model was shown when the data were simulated using true values which were not close to the central tendency of the informative priors. When a low value of M was used, the parameter was greatly overestimated because of minimal posterior updating to the prior. Conversely, when a high value of M was used the parameter was underestimated. However, as there was some posterior updating in this direction which meant the bias was less. Sensitivity of the reconstructed N_t trajectories to this large estimation bias in M was low. The sensitivity of other parameter estimates to alternative true values was generally increased when the simulated fox density was low. Because there are fewer foxes, there are more zero sighting events and therefore less information with which the model can separate true from false zeros. This could be a reason why d was not estimated as well in a low density population as when the base case set of true values was used. The underestimation of d when the true value was higher or lower than the prior median is a possible explanation for the

overestimation of N_t , as with a lower rate of successful search the fox density must be higher to explain the number of sightings.

The overestimation of r using a true value that was lower than the prior median was not unexpected given that the true value was located in the lower tail of the prior distribution. With a value at this extreme location of the prior distribution the data would need to be very informative to completely override the prior central tendency. Although the posteriors show that the prior was updated downwards in all datasets, this caused the overestimation of r . A notable feature of the alternative sets of simulations using high and low values relative to the prior medians was that convergence on the joint posterior was not as straightforward as under the base case set of values. Those datasets for which convergence was most difficult appeared to show the most bias in the parameter estimates. This was especially the situation for K . In these cases additional iterations of the Markov chains and an increased rate of thinning of the chains were required to reach satisfactory convergence. When applied to real data such diagnostics may act as a warning that the estimation model is performing poorly and that the results should be viewed as potentially unreliable given particular datasets.

3.4.2 Minimum data requirements

The culling effort data must contain enough weeks with lamping effort during the May-June periods of cub recruitment to be able to estimate r , regardless of whether an informative prior is used. The simulation-estimation analysis suggested that at least two weeks per year during these periods must contain lamping effort for the sighting rate time series to contain sufficient information. However, this is usually the most challenging time of year in which to try and sight foxes with a lamp on arable land due to increased crop cover. Some FMS estates did not lamp at all during this period, consequently these estates must be excluded from further analysis using this model because the data do not meet this requirement.

The estimation model was unable to recover N_t trajectories reliably or estimate parameters without bias from shorter time series of <2 years. Despite these time series being around 100 weekly time steps long, they only cover two cub recruitment periods. This

appears to be insufficient information to separately estimate ν and r , as shown by the negative posterior correlation between these parameters when time series are short. This highlights a further challenge to using SSMS to estimate density-dependent terms as parameters may be strongly correlated if there are not enough time steps in the data (Lebreton & Gimenez 2013). Although correlations in the joint posterior were not strong when informative priors were used with this model, there was clearly more correlation when time series were shorter.

Estimation was improved as time series became longer, and N_t trajectories were generally well estimated for time series that were ≥ 3 years long. For any length of time series, there was minimal bias in estimates of ν , r , M and d when informative priors were used. However, bias in N_0 , K and σ_p estimates was reduced only when time series were ≥ 4 years. The decision on where to set the minimum acceptable time series length was made in conjunction with the real FMS data. Only 20% of estates in the FMS contributed data for four or more years, with a further 10% of estates contributing data for between three and four years. This meant that few FMS datasets contained sufficient information to give reliable results using this model. As a compromise, a 3-year time series including at least three cub recruitment periods was taken as the minimum required length, provided that estimates of N_0 , K and σ_p from time series < 4 years were treated with appropriate caution.

In addition to overall time series length, estimates were affected by how many weeks' lamping effort there were each year. The ability of the gamekeeper to keep the fox population at a low density is also dependent upon how much culling effort is used, meaning that culling success and reliable estimation of the population dynamics are linked. Lamping is only one of a suite of culling methods available to the gamekeeper and, as the FMS data show, there is a seasonal variation in when it is used. This means the sighting rate data are quite sparse on many estates during certain times of year, as several weeks (or months) can pass without any lamping effort being used and consequently there is no sighting rate data during these periods. Weekly estimates of N_t from periods without lamping effort were often poor because without sighting rate data to fit the model to it becomes increasingly difficult to distinguish between observation and process errors. Eight weeks of lamping effort per year

was the recommended minimum data a sighting rate time series must contain, with no gap in the time series longer than nine months. Time series with little lamping effort in the first year resulted in greater N_0 estimation bias, while high effort levels during the first year resulted in minimal bias. Accordingly, consistent lamping effort during the first three months was determined to be a requirement for reliable estimation of N_0 .

3.4.3 Information from variable effort

The examination of different lamping effort schedules using a simulation-estimation approach is comparable to active adaptive management, which seeks to improve management of complex and uncertain systems by concurrently implementing a range of alternative strategies to probe and learn about the system and determine the optimal strategy (Walters 1986). The most informative data are those containing contrasts in both abundance and effort (Hilborn 1979; Magnusson & Hilborn 2007). Such data are often obtainable only by strategies that push the system to its boundaries, making them risky options in real situations. For gamekeepers on shooting estates, this would involve drastically reducing fox control effort in some years and hugely increasing it in others, which could severely affect wild bird production and have both economic and conservation costs. Adaptive probing of effort levels using simulation-estimation is a less risky alternative and, although the results are subject to the various model assumptions, it can still help gamekeepers make culling strategy decisions to enable future data to be as informative as possible (Magnusson & Hilborn 2007).

The number of foxes sighted is determined by lamping effort and the fox density, so if lamping effort is constant over time, i.e. schedule S1, and non-culling mortality, reproduction and immigration are stable, process variation in fox density is the only cause of between-year contrasts in the data. Compared to the variation in fox density which could be caused by variable lamping effort, process variation will be minimal. It was therefore expected that sighting rate time series with more variable annual lamping effort would result in improved parameter estimates. The results were consistent with this, although the reduction in bias and precision was not to the extent expected. Under lamping effort

schedules S4-S6, the greatest reduction of bias was in estimates of r . Compared to S1, the median PRB for r was reduced by over half as these schedules pushed the fox population to its extremes, making it easier to estimate density-dependent processes. Precision under S4-S6 was either similar to S1 or slightly improved. A notable exception was N_0 , for which the CV was considerably higher under S5 because there was very little lamping effort in the first two years of this schedule. Overall, S6 resulted in the least biased and most precise parameter estimates, and also the least biased weekly N_t estimates.

The improvement in estimation from S1 to S6 might not have been as large as expected as the effort multiplier values used were too extreme. Incorrect specification of the observation model can markedly affect inference using SSMs (Knappe, Jonzén & Sköld 2011), and if there are very few weeks in which there is lamping effort, i.e. under a 0.1 multiplier, the assumption that fox sightings are Poisson-distributed is tested as the variance in sightings will become increasingly unstable. In these situations the results might be improved by use of an alternative observation error distribution, e.g. negative binomial, which accounts for over- or under-dispersion. For this reason it would be prudent to examine the sensitivity of the results from the real FMS data to the Poisson observation model specification.

The effort probing findings are however consistent with Hilborn (1979), who identified the most informative data scenario in a fishery to be one that includes a period of quite heavy exploitation, followed by a period where the population is allowed to recover to an intermediate level, after which the exploitation rate increases again. Of the lamping effort schedules examined, S6 is the closest to this scenario (Table 3.2). It is also worth noting that S3, the schedule most closely representing a ‘one-way trip’ scenario, where exploitation rate gradually increases while abundance decreases and is typically the least informative (Hilborn & Walters 1992), did not perform much worse than S6 and indeed Magnusson & Hilborn (2007) reported a similar finding. The majority of FMS estates showed a year-on-year decrease in effort, which is most similar to schedule S2. The results therefore indicate that estimates from such data will be no less reliable than those that would be obtainable from data with either constant effort or large annual effort contrasts.

3.4.4 Caveats and limitations

Reliable estimation of both weekly fox density and model parameters was possible only by reducing the non-identifiability problems through use of informative priors. If appropriate informative priors were not available, estimation of M was not possible and the resulting bias in other estimates would have been unacceptably high. This would have forced the use of an alternative model without all of the key demographic processes. A simplification of the depletion model structure considered in lieu of using informative priors was to combine non-culling mortality and immigration rates into one parameter. This option was not considered further because 1) immigration is a key process to the dynamics of a culled population requiring explicit estimation, 2) it would not be possible to assess the relative importance of non-culling mortality to total mortality, and 3) determining density-dependence becomes very complicated. An approach which would provide identifiable estimates of all the demographic parameters is integrated population modelling (Abadi *et al.* 2010a; Schaub & Abadi 2011), but in addition to count data such as those in the FMS, mark-recapture data are required. Such data are unlikely to ever be available from a culled population, unless there is a time period without culling during which gamekeepers would allow foxes to be captured for tagging and release.

Formulation of the model required a number of assumptions to be made. As introduced above, the lack of age-structured data in the FMS dictated the assumption that demographic parameters (v , r and M) did not vary with age. As there is conflicting evidence about whether non-culling mortality rate and cub production rates vary among age classes (Heydon & Reynolds 2000b; Soulsbury *et al.* 2008) this was considered an acceptable assumption for r and M . Age-specific variation in v is probable as juveniles form 60% of the regional source population (Devenish-Nelson *et al.* 2013). Nevertheless, if r and M truly are age-independent rates, then the effect on the population dynamics of a larger than assumed proportion of juveniles immigrating onto an estate would be minimal.

For fox density estimates, a more important assumption with respect to immigration is that it occurs at a constant rate year-round and does not vary with the dispersal period, i.e.

there is no strong seasonality in immigration rate due to it consisting mainly of dispersing juvenile foxes. The FMS suggests that more foxes are culled during the August-October period (Fig. 2.3) which could imply that dispersing foxes were causing the increase in culled foxes, but with October-January being the peak dispersal period (Macdonald & Reynolds 2004) this overlap is not clear. Additional confounding factors are that the fox population is naturally at its highest in late-summer following cub recruitment, and lamping effort is also at its highest during the August-October period, so larger fox bags would be expected then.

Without additional information on seasonal variation in immigration rates of foxes with which to parameterise the seasonal timing of immigration, and as field evidence indicates that both adults and juveniles may move during the summer, the assumption must be that immigration rate is constant. Otherwise additional model parameters would be required to account for the seasonality, which would further increase identifiability problems. If immigration occurred only during the dispersal period, the expected effect of assuming constant immigration would be that the immigration rate of foxes would be underestimated during the dispersal period. In the case of all other parameters being constant, this would lead to underestimation of fox density and overestimation of the effectiveness of culling at this time of year, and *vice versa*. Sensitivity to this assumption must therefore be examined when fitting the model to the real FMS data.

Immigration was modelled using a net immigration term, but emigration was not explicitly modelled within this model structure. Instead, emigration was implicitly assumed to be incorporated into the model via net immigration, with emigration rate also likely to be technically confounded with non-culling mortality rate, especially for smaller estates. However, the expectation for a sink population, such as a local fox population subject to restricted area culling, is that emigration will be minimal. Therefore any errors arising through not explicitly incorporating emigration into this model structure may also be expected to be minimal.

Density-dependence is a key consideration in the management of exploited species (Guthery & Shaw 2013). Accounting for density-dependence in cub production and immigration assumes there is a carrying capacity density at which resource availability limits

the fox population. This is reasonable as higher fox densities are found where food is more available, e.g. in urban environments. The assumption in using logistic terms to model this density-dependence is that there is a linear decline with density in population growth by cub recruitment or in immigration. For territorial animals such as foxes a non-linear relationship is more realistic because growth is likely to be relatively unaffected by increasing fox density while there is vacant territory space, but once crowding occurs at higher densities the growth will slow rapidly as the population nears carrying capacity. The theta-logistic model allows for this convex relationship (Gilpin & Ayala 1973; Sibly *et al.* 2005). However, as the extra parameter necessary for this realism is often difficult to estimate and can lead to unreliable inferences (Clark *et al.* 2010), and this model already appears to be on the limits of identifiability, theta-logistic terms for density-dependence were not considered further.

The use of a *per capita* birth rate parameter to model the recruitment of weaned cubs meant that it was assumed that there was no non-culling mortality of cubs within earths. No data are known to exist on non-culling mortality from birth to weaning, so relaxing this assumption meant incorporating a cub mortality rate parameter into the estimation model. Estimation of a cub mortality rate was attempted during initial stages of model formulation but it was not identifiable due to strong correlation with r . Cubs were assumed to become vulnerable to lamping effort from eight weeks onwards. This assumption is supported anecdotally by the FMS data, as across all estates, only one cub was recorded as being killed by lamping before the start of May and so was within the weaned cub distribution.

Other key assumptions relate to the scaling parameter. This parameter represents the product of the search rate by a gamekeeper across an estate and the sighting probability (see Chapter 6), and defines a proportional relationship between sighting rate and fox density. An assumption of this model structure is that the scaling parameter does not vary with fox density. Failure of this assumption can cause the model to make incorrect predictions, either because the sighting rate shows hyperdepletion and declines rapidly over time compared to density, or shows hyperstability and stays high as density declines. To incorporate such non-linearity in the relationship between sighting rate and fox density a possibility would be to assume that fox sightings are predicted by the Holling disc equation (Holling 1959a).

Handling time in this equation would represent effective search time lost per fox encountered, e.g. due to time spent determining if a shot is safe, collection of shot foxes for age or sex determination, or refractory time caused by scaring of foxes within hearing distance of each shot taken. This therefore sets an upper limit on the number of possible fox sightings for a given lamping time. However, unless assumptions can be made about the handling time and its variability among, it is an additional parameter that must be estimated. It is unlikely to be an identifiable parameter unless a strongly informative prior was available, and given a lack of data upon which to construct such a prior this option was not pursued.

The scaling parameter is also assumed to be constant over time. Inconstant sightability is a potentially large source of error when using estimation methods such as this which are based upon changes in sighting rate (or catch per unit effort, Hilborn & Walters 1992). The probability of a sighted fox being killed in the FMS was only 30%; if all sighted foxes were shot at it would be expected that sighting probability would decrease over time due to spotlight avoidance behaviour by foxes that are repeatedly shot and missed (Heydon, Reynolds & Short 2000). It is actually often not possible to make a safe shot on a sighted fox, which contributes to the low probability of lamping success, so the actual proportion of foxes shot at and missed is probably fairly low. In addition, a high turnover in the fox population due to culling, including that by methods other than lamping, e.g. snaring, meant that this effect was not expected to be major. There may also be seasonal variation in sighting probability for foxes due to visibility changing, e.g. due to crop cover during the summer. This could potentially lead to biased estimates of N_t , during the summer, but without covariate data on habitat types that foxes were seen in or a field experiment to determine if the sighting probability does vary seasonally, it is not possible to assume otherwise that it is not constant. To avoid any bias, sighting rate data from the summer period could be ignored, but as data during this period is necessary for reliable estimation of cub recruitment this option was not possible.

3.5 Tables

Table 3.1. Prior probability distributions for estimated model parameters used in simulation-estimation analysis.

Model parameter	Vague priors		Informative priors	
	Distribution	Parameters	Distribution	Parameters
N_0	~ uniform	lower = 0.001 upper = 13.9	not specified	-
K	~ uniform	lower = 0.001 upper = 13.9	not specified	-
v	~ uniform	lower = 0 upper = 1	~ lognormal	Median = $\ln(0.045)$ CV = 0.8
r	~ uniform	lower = 0 upper = 6	~ lognormal	Median = $\ln(3.0)$ CV = 0.33
M	~ uniform	lower = 0 upper = 0.1	~ lognormal	Median = $\ln(0.009)$ CV = 0.6
d	~ uniform	lower = 0 upper = 10	~ lognormal	Median = $\ln(2.0)$ CV = 0.6
σ_p	~ uniform	lower = 0.001 upper = 0.5	not specified	-

Table 3.2. Annual multiples of scaled mean weekly effort values used to generate the alternative lamping effort schedules.

Lamping effort schedule	Year 1	Year 2	Year 3	Year 4	Year 5
S1	1x	1x	1x	1x	1x
S2	1.6x	1.3x	1x	0.7x	0.4x
S3	0.5x	0.75x	1x	1.3x	1.6x
S4	2.5x	0.1x	0.2x	1x	1.3x
S5	0.1x	0.2x	2.5x	1.3x	1x
S6	1x	2.5x	0.1x	0.4x	1x

Table 3.3. True parameter values used to generate the base case simulated data.

Parameter	Symbol	Value	Units
Initial density	N_0	2.0	fox km ⁻²
Carrying capacity	K	4.0	fox km ⁻²
Immigration rate	ν	0.046	fox km ⁻² wk ⁻¹
Per capita birth rate	r	2.8	cubs fox ⁻¹ yr ⁻¹
Instantaneous non-culling mortality rate	M	0.009	wk ⁻¹
Scaling parameter	d	2.0	km ² hr ⁻¹
Process error standard deviation	σ_p	0.15	-
Estate area	A	10	km ²
Probability of a sighted fox being killed	p_l	0.30	-
Probability of snaring success per fox per week	p_s	0.05	-
Probability of death at the earth per cub	p_c	0.20	-

Table 3.4. Mean posterior coefficient of variation (CV) for each parameter across 20 simulated populations under alternative annual lamping effort schedules.

Lamping effort schedule	N_0	K	ν	r	M	d	σ_p
S1: 1x, 1x, 1x, 1x, 1x	0.51	0.65	0.13	0.20	0.60	0.11	0.29
S2: 1.6x, 1.3x, 1x, 0.7x, 0.4x	0.52	0.57	0.12	0.19	0.60	0.12	0.30
S3: 0.5x, 0.75x, 1x, 1.3x, 1.6x	0.51	0.60	0.12	0.19	0.59	0.11	0.31
S4: 2.5x, 0.1x, 0.2x, 1x, 1.3x	0.50	0.45	0.11	0.19	0.56	0.12	0.33
S5: 0.1x, 0.2x, 2.5x, 1.3x, 1x	0.61	0.44	0.12	0.20	0.57	0.13	0.29
S6: 1x, 2.5x, 0.1x, 0.4x, 1x	0.49	0.50	0.12	0.19	0.57	0.11	0.31

Table 3.5. Mean Percent Relative Bias in the medians of the marginal posterior probability distributions from 20 populations relative to different sets of true parameter values used to simulate them: the base set of values in Table 3.3 and two alternative sets of values; one giving a low fox density population ($0.5[N_0, v, r, M], 1.5[d]$) and one giving a high fox population ($1.5[N_0, v, r, M], 0.5[d]$). K and σ_p were unchanged from the base case. All estimation models used the same informative priors on v, r, M and d .

Parameter	Base case	Low density	High density
N_0	15.2	19.2	14.8
K	14.9	1.3	38.0
v	3.3	3.6	3.6
r	9.4	46.9	-9.3
M	8.9	118.7	-15.5
d	-0.3	-12.3	-4.9
σ_p	6.4	8.6	-2.3
\widetilde{N}_t	3.3	9.2	11.1

3.6 Figures

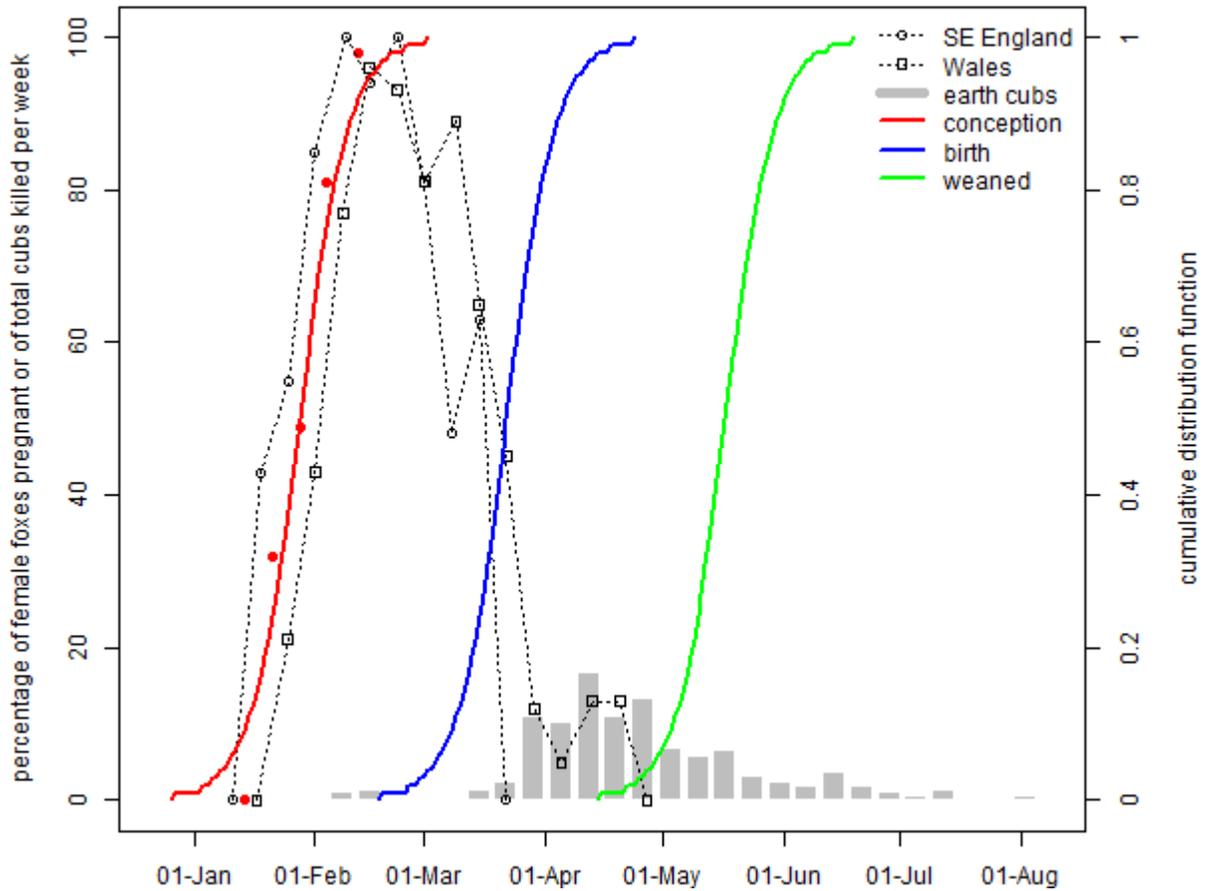


Figure 3.1. Data from two British fox populations on the percentage of female foxes that were pregnant at different times during the breeding season (Lloyd 1980) are summarised, with mean dates and percentages (red points) used to fit a cumulative logistic distribution to show the percentage of the female population that had conceived over time. The distribution of births was obtained assuming a gestation period of 52 days, from which the distribution of weaned cubs was obtained by assuming that all cubs were weaned by eight weeks old. The weaned distribution describes when cubs become vulnerable to lamping effort.

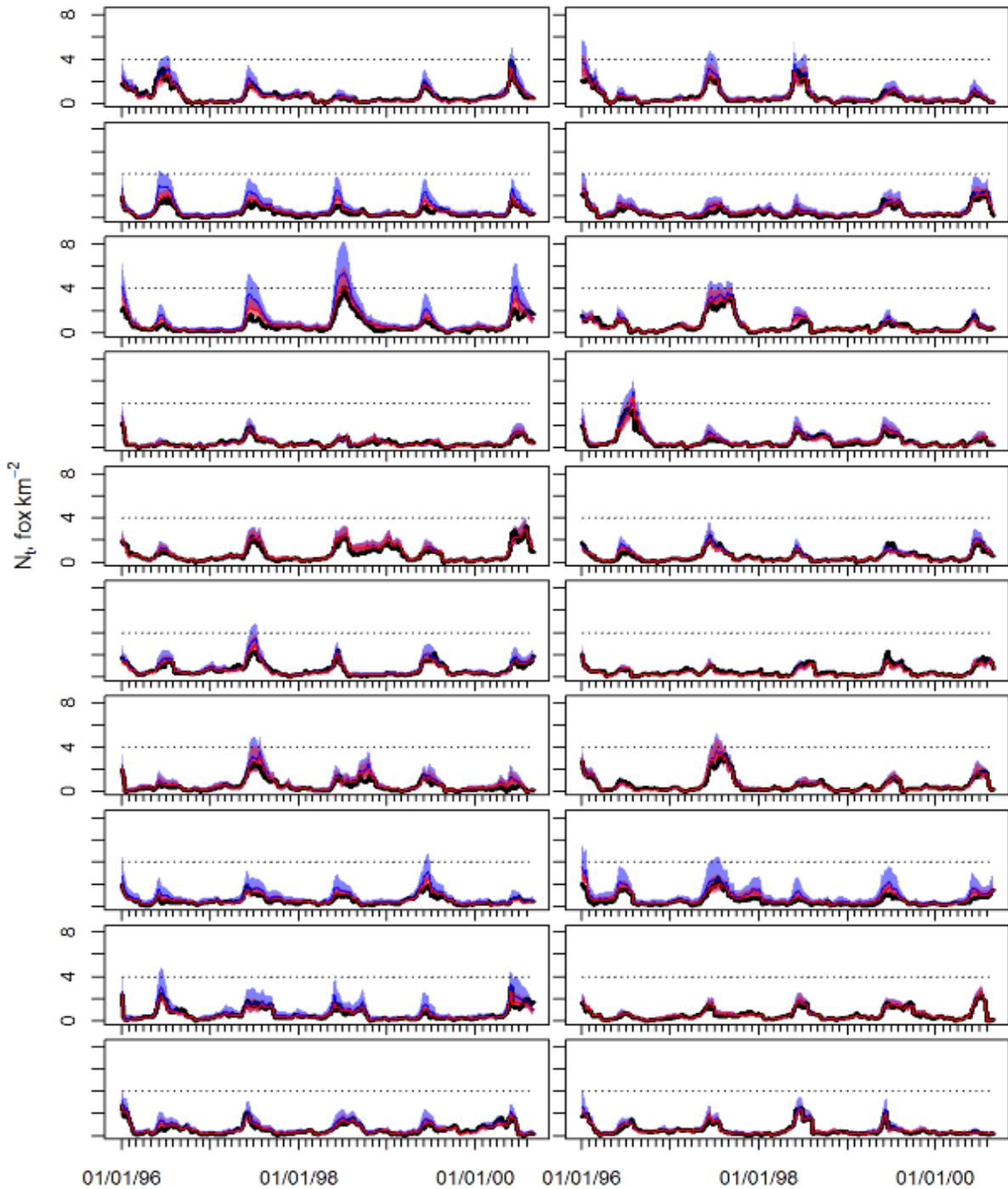


Figure 3.2. Fox density time series from 20 populations simulated on a weekly time step under a seasonal culling strategy (black). The medians of the posterior probability distributions for weekly fox density estimated using an estimation model with either a) vague priors (blue) on all model parameters, or b) informative priors (red) on ν , r , M and d , with vague priors on the other parameters, are plotted. Blue and red shading shows the 80% credible intervals for vague prior and informative prior models, respectively. Dotted line shows true value of K .

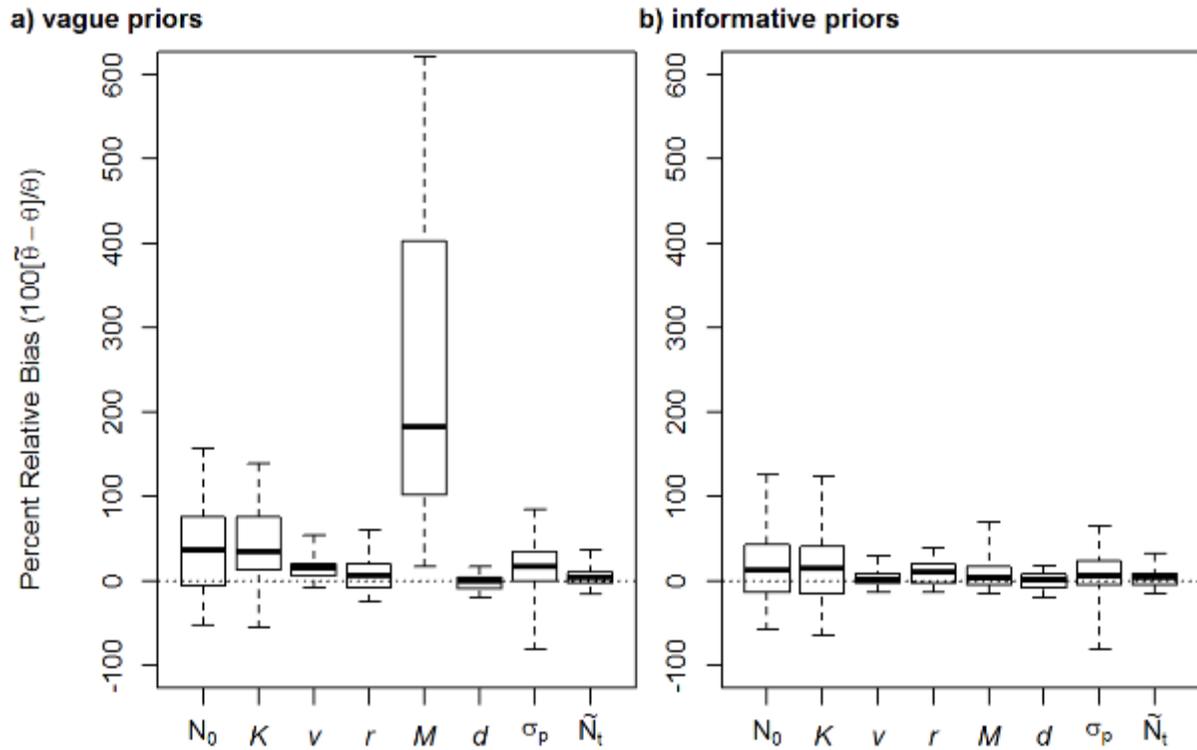


Figure 3.3. Distributions of percent relative bias (PRB) in the median of the marginal posterior probability distributions from 20 populations relative to the true parameter values used to simulate the populations on a weekly time step under a seasonal culling strategy. In addition to the PRB in parameter estimates, the mean PRB in weekly N_t is shown. The estimation model used either a) vague priors on all model parameters, or b) informative priors on v , r , M and d , with vague priors on the other parameters. The median PRB for each parameter is shown as a black bar, boxes represent the interquartile range (IQR), and whiskers represent the range of PRB.

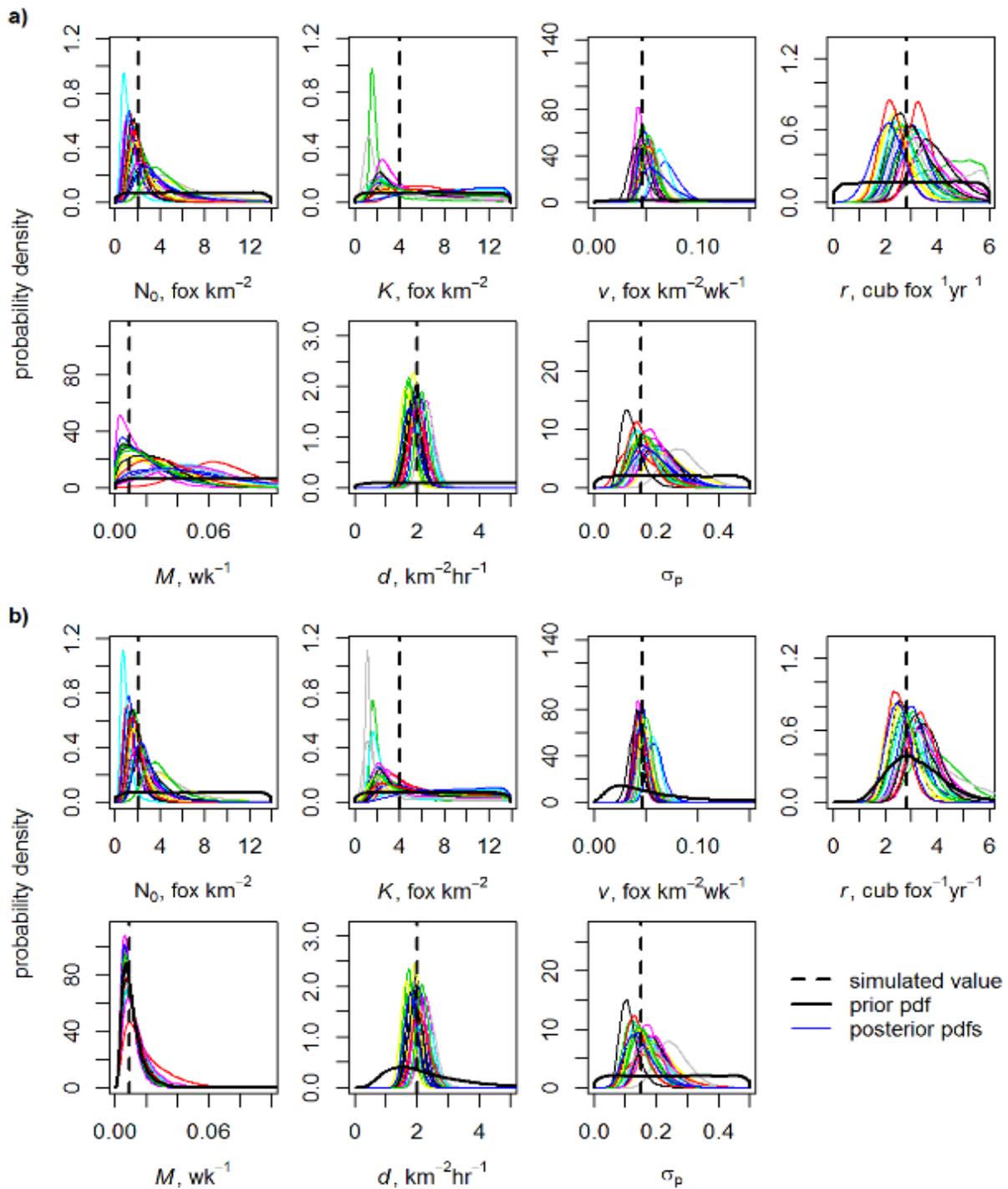


Figure 3.4. Profiles of the marginal posterior probability distributions of parameters estimated from 20 populations simulated on a weekly time step under a seasonal culling strategy. The estimation model used either a) vague priors on all model parameters or b) informative priors on v , r , M and d , with vague priors on the other parameters. Each coloured line represents one simulation; solid black line represents the prior, vertical dashed line represents the true parameter value used in the simulations.

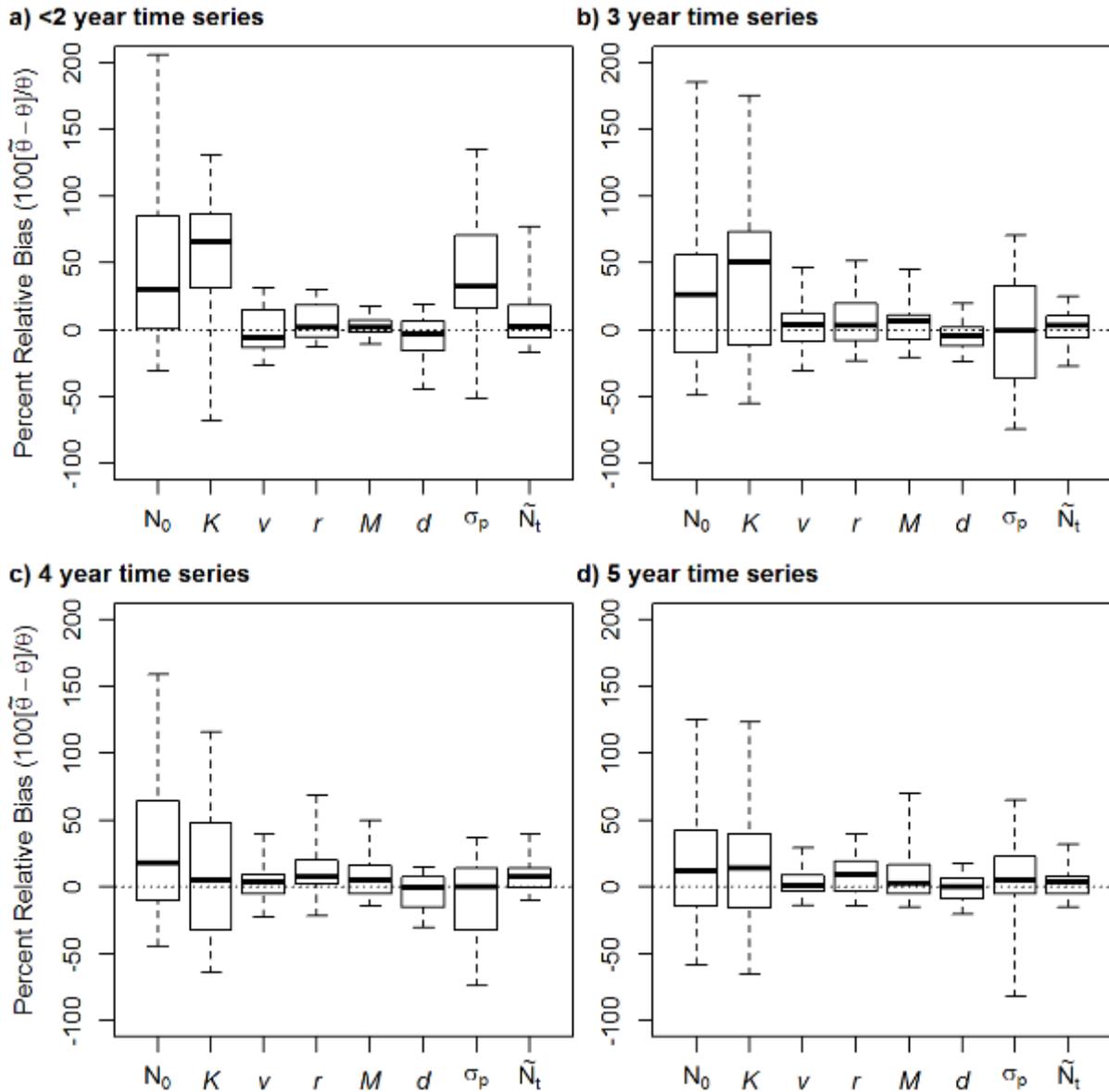


Figure 3.5. Distributions of percent relative bias (PRB) in the median of the marginal posterior probability distributions from 20 populations relative to the true parameter values used to simulate the populations on a weekly time step under a seasonal culling strategy. In addition to the PRB in parameter estimates, the mean PRB in weekly N_t is shown. Differences in PRB due to length of sighting rate time series that were a) two years or less, b) three years, c) four years, or d) five years long are shown. The estimation model used informative priors on v , r , M and d , with vague priors on the other parameters. The median PRB for each parameter is shown as a black bar, boxes represent the interquartile range (IQR), and whiskers represent the range of PRB.

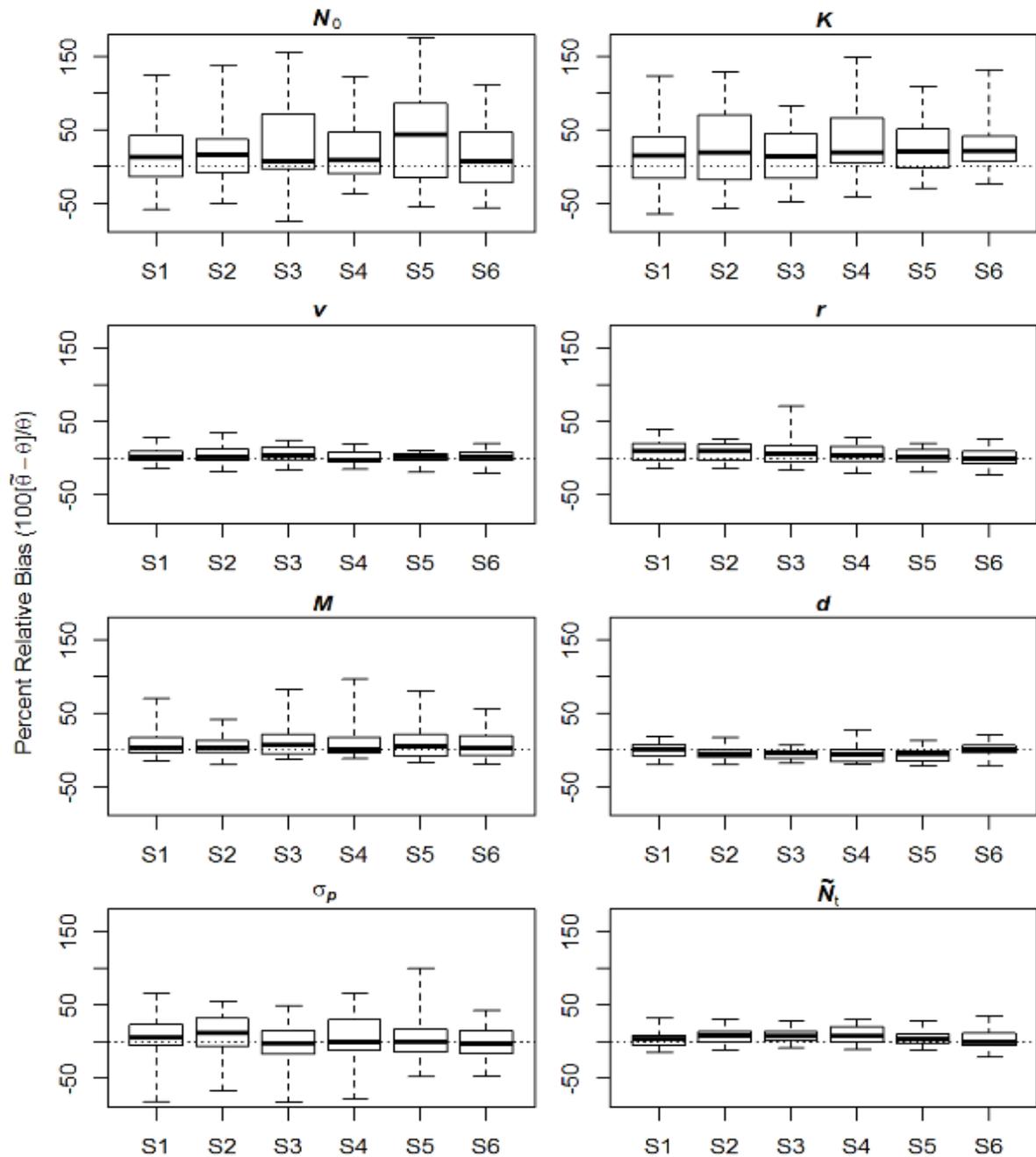


Figure 3.6. Distributions of percent relative bias (PRB) in the median of the marginal posterior probability distributions from 20 populations relative to the true parameter values used to simulate populations on a weekly time step under a seasonal culling strategy. The amount of lamping effort was varied within a five-year time series by multiplying mean annual lamping effort by different values to give alternative schedules (S1 to S6). In addition to the PRB in parameter estimates, the mean PRB in weekly N_t is shown. The estimation model used informative priors on v , r , M and d , with vague priors on the other parameters. The median PRB for each parameter is shown as a black bar, boxes represent the interquartile range (IQR), and whiskers represent the range of PRB.

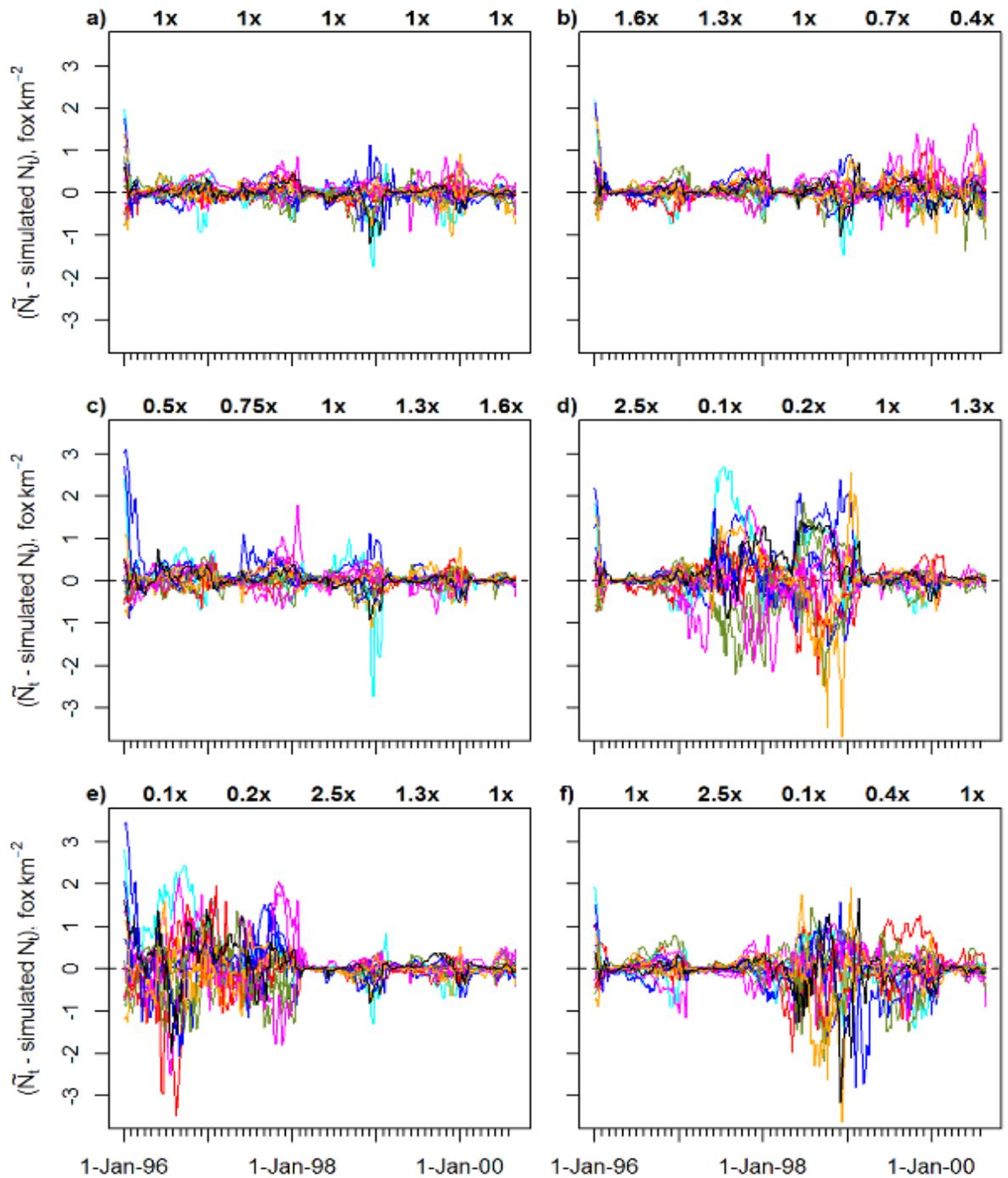


Figure 3.7. Differences between the median of the marginal posterior probability distribution for weekly fox density and the simulated ‘true’ weekly fox density from 20 populations to highlight the estimation error (as departure from zero) under variable annual lamping effort. The annual effort variations were achieved by multiplying mean annual lamping effort by different values to give alternative schedules (plots a-f). The estimation model used informative priors on v , r , M and d , with vague priors on the other parameters. Each coloured line represents one simulation.

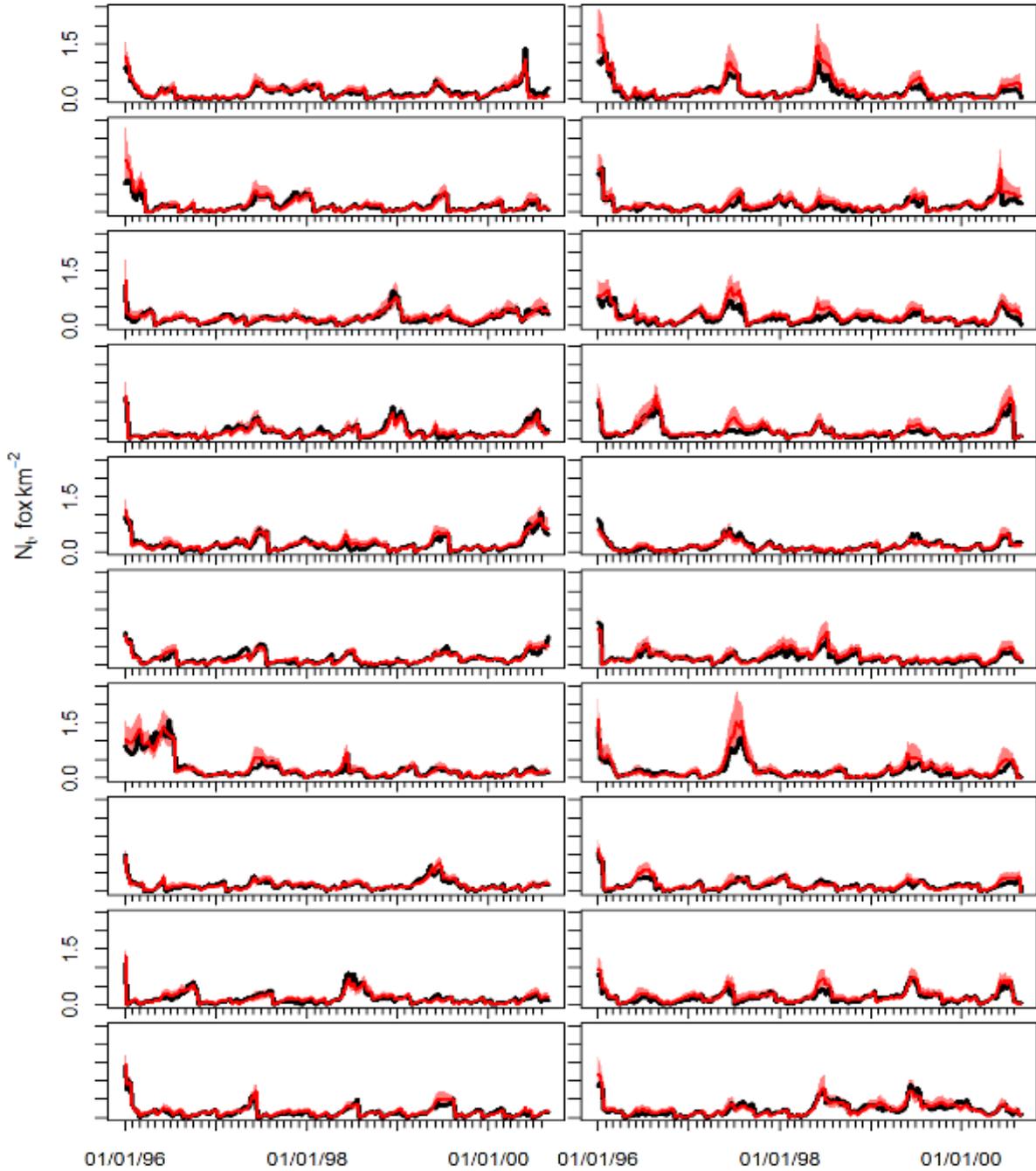


Figure 3.8. Fox density time series from 20 populations simulated on a weekly time step under a seasonal culling strategy (black). Data were simulated using true values 0.5 times the base case values for N_0 , v , r and M , and 1.5 times the base case value for d in Table 3.3, giving lower fox densities relative to K (4 fox km^{-2}) than the reference set in Figure 3.2. The medians of the posterior probability distributions for weekly fox density estimated using an estimation model with informative priors (red) on v , r , M and d , with vague priors on the other parameters are plotted. Red shading shows the 80% credible interval.

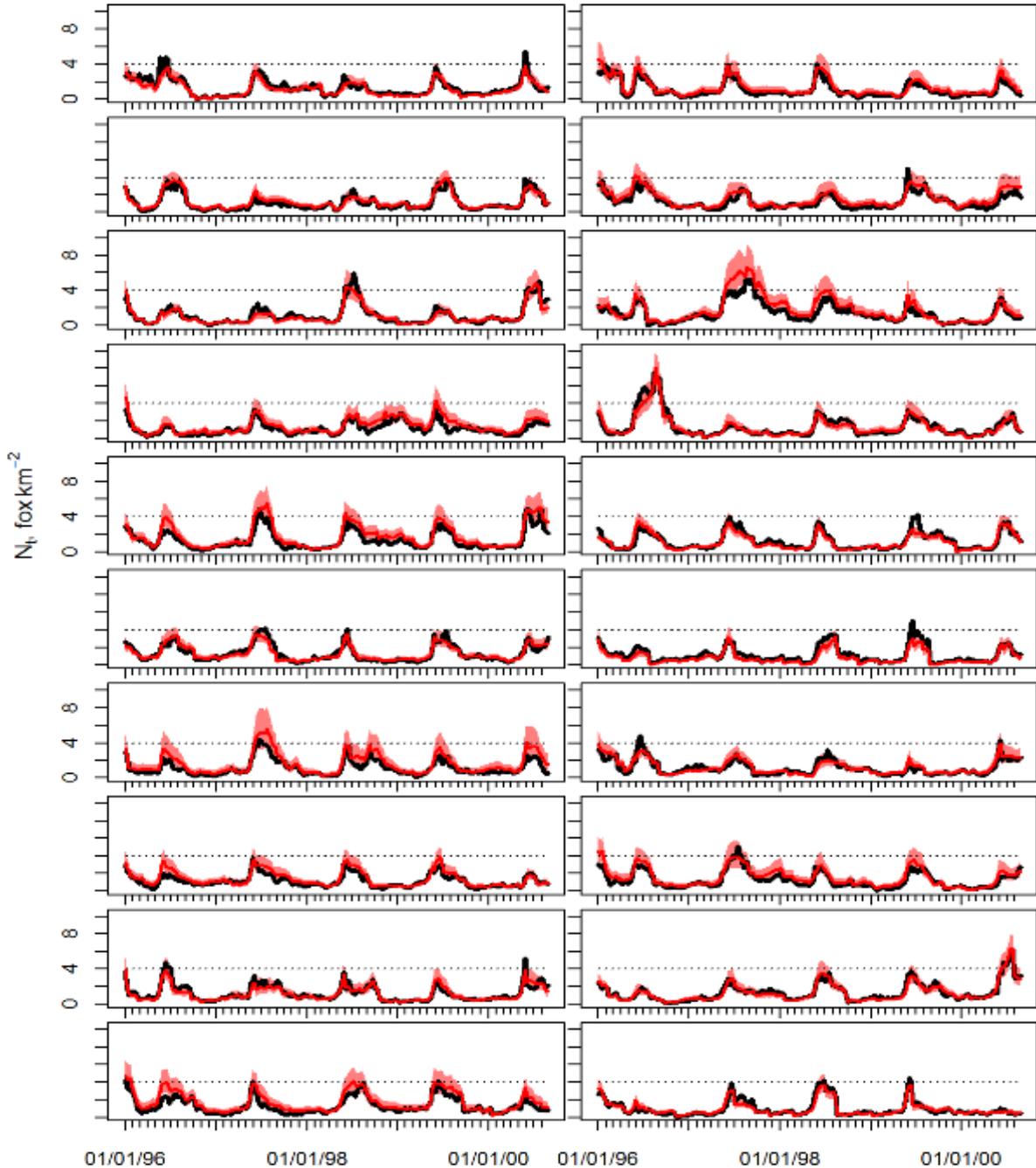


Figure 3.9. Fox density time series from 20 populations simulated on a weekly time step under a seasonal culling strategy (black). Data were simulated using true values 1.5 times the base case values for N_0 , v , r and M , and 0.5 times the base case value for d in Table 3.3, giving higher fox densities relative to K (4 fox km^{-2}) than the reference set in Figure 3.2. The medians of the posterior probability distributions for weekly fox density estimated using an estimation model with informative priors (red) on v , r , M and d , with vague priors on the other parameters are plotted. Red shading shows the 80% credible interval. Dotted line shows true value of K .

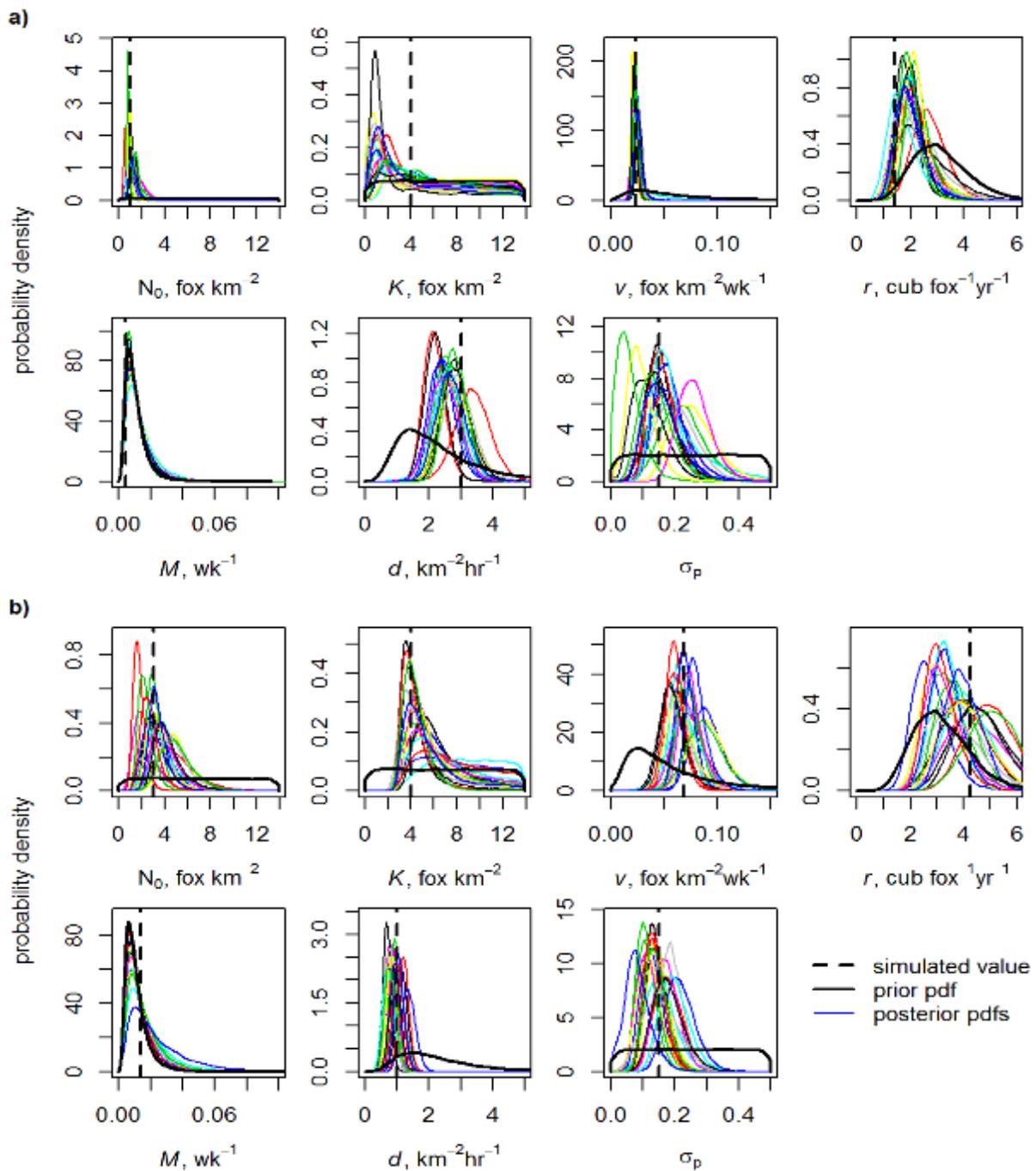


Figure 3.10. Profiles of the marginal posterior probability distributions of parameters estimated from 20 populations simulated on a weekly time step under a seasonal culling strategy. Data were simulated using true values a) 0.5 times the base case values for N_0 , v , r and M , and 1.5 times the base case value for d in Table 3.3, or b) 1.5 times the base case values for N_0 , v , r and M , and 0.5 times the base case value for d . The estimation model used informative priors on v , r , M and d , with vague priors on the other parameters. Each coloured line represents one simulation; the solid black line represents the prior, vertical dashed line represents the true parameter value used in the simulations.

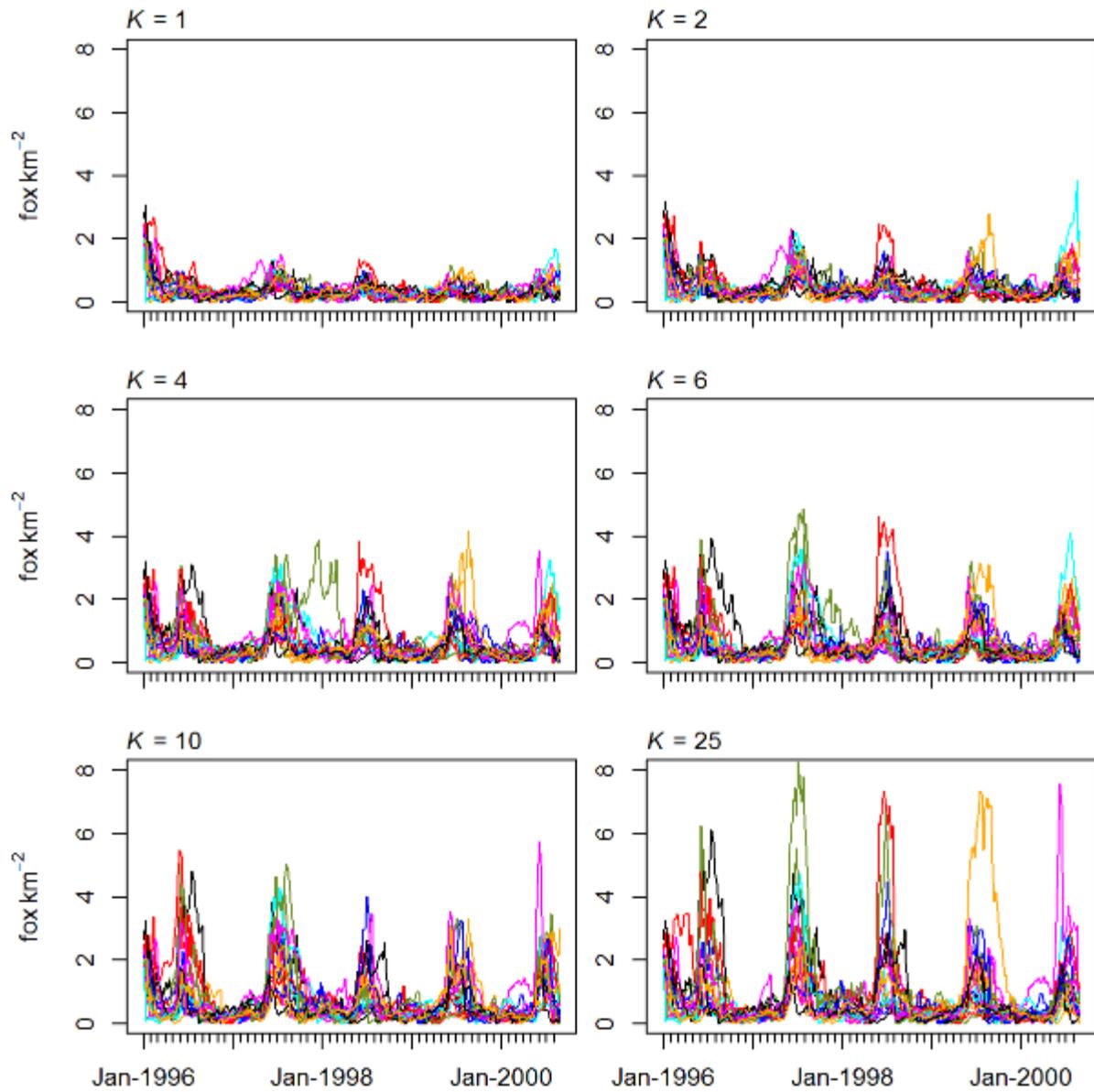


Figure 3.11. Simulated fox density of 20 populations under different carrying capacity values. All other parameter values were as defined in Table 3.3 (reference case is $K=4$ fox km⁻²).

Chapter 4: Estimating priors for immigration rate during restricted-area fox control

4.1 Introduction

Like many vertebrate pests, red fox (*Vulpes vulpes*) populations are controlled throughout much of their range to reduce their impact on prey species and the incidence of disease (Macdonald & Reynolds 2004). In rural Britain, fox control is particularly associated with shooting estates with the aim of benefitting small game populations for harvesting (Tapper 1992; Reynolds & Tapper 1996; Heydon & Reynolds 2000a). Models of population dynamics, such as the open-population depletion model formulated in Chapter 3, can potentially allow the effect of management on local-scale density to be determined from data on culling effort and success. However, ambiguity in management-related outputs can arise in population dynamics models when uncertainty exists over the correct values to apply for key parameters (Bryan 2012).

Culling data are often uninformative about key model parameters, particularly if time series are too short or sparse. In such situations, use of a Bayesian modelling framework and explicitly incorporating prior knowledge via informative prior probability density functions, can reduce uncertainty and improve estimation performance by constraining the model within reasonable biological limits. The concerns with use of informative priors in Bayesian models are their subjectivity and potential to overwhelm posterior estimates if they are too informative relative to the data (Dennis 1996). Provided care is taken to ensure that prior information is used in a logical and sensible manner, these concerns must be weighed against the advantage of making inferences about populations on which data are scarce (Martin *et al.* 2013). The value of using suitable informative priors has been shown whether they are derived from expert knowledge (Martin *et al.* 2005; Kuhnert, Martin & Griffiths 2010), published data (McCarthy & Masters 2005; Martin *et al.* 2013), or other analytical methods (McAllister, Pickett & Babcock 2001; McAllister, Stanley & Starr 2010).

Immigration is a key demographic process in pest populations that can strongly impact control strategy choices due to source-sink dynamics (Smith 1985; Hone 1994). If

the immigration rate from outside a culled area is high then culled animals may be replaced just as quickly as they are removed, and the area becomes a sink for the surrounding area (Reynolds, Goddard & Brockless 1993; Robinson *et al.* 2008). Culling has both animal welfare and economic costs. If culling effort does not result in the intended level of control of population density then this effort becomes difficult to defend. To achieve the same level of fox population reduction on an estate where immigration rate is high, the level of culling effort must be greater than on estates where foxes are replaced at a slower rate. Being able to make reliable inferences about immigration rate on each estate is therefore vital to determining culling effort levels that can result in effective control of a local fox population. The use of an informative prior for immigration rate can improve these inferences (Chapter 3).

Unfortunately, immigration rate is a notoriously difficult parameter to estimate because immigrants must be distinguished from resident individuals (Abadi *et al.* 2010b). As a result, little prior knowledge exists about immigration rates in fox populations or about factors such as habitat and surrounding fox density which may affect immigration rates. The methods most commonly used to estimate immigration rely on marking individuals. Immigration rates may be estimated from direct counts of unmarked individuals in long-term intensive studies where all individuals in the population are marked each year (Slough & Mowat 1996); or from the collection of capture-recapture data on marked individuals and, depending on how the data were sampled and which age classes were marked, using different models to infer immigration (Nichols & Pollock 1990; Peery, Becker & Beissinger 2006; O'Hara, Lampila & Orell 2009). Capture-recapture data may be combined with population counts or indices to estimate immigration using integrated population models (Besbeas *et al.* 2002; Abadi *et al.* 2010b). It is also possible to use molecular genetic techniques to detect immigration by determining genetic differentiation between multilocus genotypes of individuals in different areas (Wandeler *et al.* 2003).

There are several problems with using these methods for a cryptic species such as the fox. Capture using live-capture traps is difficult, so intensive effort is required to mark or take genetic samples from individuals. In Britain the approved capture methods for foxes are

free-running neck snares and cage traps, but both methods have capture rates below 1 capture/100 trap-nights, and usually an order of magnitude lower (Baker *et al.* 2001; Short *et al.* 2012). A consequence of low capture (and recapture) rates is that to get a large enough sample of marked foxes for capture-recapture techniques to be applicable, trapping must take place over such an extended time period that it becomes difficult to fulfil assumptions underlying these mathematical models (Sadler *et al.* 2004). Finally, there is an obvious conflict between the capture and release of foxes and fox control, so estimation of immigration rate using these methods is scarcely feasible in culled populations. Clearly there is a need for an alternative approach using data from culled populations to construct an informative prior for immigration rate.

In Britain, many shooting estates volunteer data to the National Gamebag Census (NGC) on the annual numbers of game and predator species killed (Tapper 1992). While the NGC represents the richest source of trend data on rural fox populations (Battersby 2005), it may also contain information about the annual rate of immigration. At equilibrium, the fox population satisfies the annual mass balance where cubs born per area plus immigrants per area equals non-culling deaths per area plus culling removals per area. The annual fox cull on each estate can therefore include both net local production (i.e. births minus non-culling deaths) and immigrant foxes. On a small estate there is less area on which resident foxes can set up territories and produce cubs, so net local production is expected to be small. As the estate size drops to zero, the net local production component of the annual cull should thus diminish relative to the immigration component. The relationship between cull and estate area is expected to increase non-linearly for two reasons. First, the ratio of boundary to area increases geometrically as estate area decreases, and so the ratio of immigration rate to net production rate from the area within the estate should also increase as estate area decreases. This would result in relatively higher numbers of culled foxes on small estates due to proportionally more immigrants. Second, the number of gamekeepers employed does not increase linearly with estate area. As estate size increases, the effort of a gamekeeper is spread more thinly, until there is a clear need to employ an additional gamekeeper. On small estates, effort is therefore more concentrated and the cull is expected to be large relative to the area. Standardisation to remove the area effect on the cull will result in a negative

relationship between the annual cull density (foxes killed km⁻²) and estate area. On a hypothetical estate with extremely small area, the cull density is therefore expected to primarily reflect immigration rate. Annual immigration rate is hence taken to be equal to the intercept of a regression model of cull density on estate area.

The immigration pressure experienced on a managed estate is assumed to be a function of fox density and productivity in the surrounding area. If the source population of foxes near the estate is large, immigration rates will be higher and *vice versa*. Both fox density and productivity are ultimately determined by food resources, but culling pressure also has a complex influence. At local scales, culling on neighbouring estates will directly reduce immigration rate by reducing the density of potential source populations nearby. Culling across larger regions might also be expected to reduce immigration rates. Fox culling pressure is influenced by regional variation in culling practices (Tapper 1992; Heydon & Reynolds 2000a). A study of three regions (East Anglia, East Midlands, Wales) suggested that culling was a key determinant of fox density at this scale. Fox density predictions made by extrapolating on the basis of land-use (Harris *et al.* 1995) matched observed density in only 2/3 regions, and did not explain observed differences in productivity. The region with highest historical culling pressure (East Anglia) had a fox density considerably lower than predicted from land-use and high productivity (Heydon, Reynolds & Short 2000); this was matched by a high reported cull, chiefly taken on shooting estates which formed 40% of the region by area. The study indicated that culling would influence immigration rates directly by reducing density at a regional scale, but also indirectly by relieving density-dependent effects at this scale (Heydon & Reynolds 2000b). In contrast, variation in fox density between seven landscape types across Britain was found to be closely related to habitat variables in six of them, while relationships of density with culling indices in these landscapes were ambiguous (three positive and one negative, Webbon, Baker & Harris 2004). The contradiction between these studies is most probably due to interactions between their scales (regional vs. landscape), but indicates that both culling pressure and habitat-related variables, e.g. prey availability, are expected to be important determinants of fox density and therefore of immigration rate.

Annual fox bags from the NGC were expected to include some variability due to regional culling pressure, as well as reflecting variable local culling effort. It was hypothesised that any remaining variation in fox bags could be explained by immigration rate in different landscape types, which were assumed to encompass habitat-related features such as food resources. Therefore, the aims of this chapter were to 1) use annual fox bag records from the NGC to estimate immigration rates of foxes onto estates; 2) determine whether immigration rate varies with landscape type; and 3) use these analyses to construct an informative prior for immigration rate to use in population dynamics modelling.

4.2 Methods

4.2.1 Landscape categorisation

Britain covers a diverse range of habitats that may be grouped for a variety of objectives, such as ecological survey. The landscape categorisation used in these analyses followed Webbon *et al.* (2004), who used faecal density counts to estimate fox density in seven different landscapes (arable a, arable b, arable c, pastoral a, pastoral b, marginal upland, upland). This landscape categorisation was based upon groupings of ‘land classes’ based on ecological characteristics (Bunce *et al.* 1996a; Walsh & Harris 1996). In national surveys since 1978, the Institute of Terrestrial Ecology (now Centre of Ecology & Hydrology) has classified all 1 km squares into strata, or land classes, based upon climatic, topographical, human geographical and geological attributes (Bunce, Barr & Whittaker 1981; Bunce *et al.* 1996b).

To construct an informative prior for use with data from the 1996-2000 period of the Fox Monitoring Scheme, the Countryside Survey 2000 data (CS2000) were used to provide the desired overlap. This dataset was also the earliest available for download at the time of analysis. The use of CS2000 complicated the landscape categorisation. Prior to this, the 1990 survey used the original 32 land classes, but in 1998 this classification was revised to 40 classes to separate strata in England and Wales from those in Scotland for the CS2000 (Barr 1998). This meant regrouping of land classes was necessary to obtain the original landscape categorisation for comparison with Webbon *et al.* (2004). Most of the ‘new’ land

classes were assigned to the same group, with the only land class 7 (arable c), land class 25 (pastoral a) and land class 33 (arable c) requiring grouping decisions to be made based upon reclassification of previous land classes. The map resulting from this landscape categorisation (Figure 4.1) was very similar to the original categorisation (Bunce *et al.* 1996a; Walsh & Harris 1996), with slight differences in total area reflecting land use changes between the 1990 and 2000 surveys.

4.2.2 NGC data

The NGC database was queried for shooting estates which submitted annual fox cull records during the 1996-2000 period. A total of 535 estates submitted data for at least one of these years (extracted on 29 July 2009). Data were summarised for each estate by calculating the mean area (A) and mean number of foxes killed per year (C). This dealt with those estates which did not contribute data consistently (332 estates did not contribute for all five years) and also those estates for which the area of the shoot changed over time as new parcels of land are bought, sold or otherwise incorporated into the managed area (out of 1800 annual records, 81 showed a change of estate area from one year to the next). Use of mean data also smoothed the unknown differences in fox culling effort during this period.

Each estate was classified into one of the seven landscape categories. Some larger estates covered more than one landscape: for those estates the category with the largest proportion of total area was chosen. This process was complicated by only 27 estates having digitally mapped boundary data, with the majority of estates having simply submitted an area and a grid reference location. For all estates a landscape categorisation determined by a circular buffer of the estate area centred on the grid reference location could be calculated within a geographical information system (GIS, MapInfo Professional 9.5, Pitney Bowes Software Ltd., Windsor, UK, 2008). For the subset of 27 estates for which there were boundary data, the landscape categorisation determined by the boundary was compared to the categorisation determined by the circular buffer using compositional analysis (Aitchison 1986; Aebischer, Robertson & Kenward 1993). This analysis was performed using the ‘compana’ function from the adehabitat package (Calenge 2006) in the R statistical software (R Core Team 2013).

4.2.3 Estimation model

Estimation of immigration rate from the NGC data used a regression model relating the fox cull density (D = number of foxes killed annually / estate area) to estate area A . The estimated intercept was assumed to be equal to the annual immigration because as the area approaches zero there is expected to be no net local production of foxes. The regression model also assumes population equilibrium over time, i.e. that the number of foxes killed annually on each estate is sustainable. Initial data exploration suggested that a better fit to the data was achieved using a log-linear version of the model with $\ln(D)$ as the dependent variable. A desirable feature of using a log-linear model is that the estimated intercept is in natural log-space, meaning once transformed into the same real-space as the cull density, immigration rate will take only positive values. A log-log model was not considered because the estimated intercept is undefined in real-space for zero area, thus giving an infinite estimate of immigration rate.

A Bayesian hierarchical framework was used to account for effects of landscape category on immigration rate. This makes the assumption that the regression parameters for each category are exchangeable into a common cross-category distribution. The category parameters are given a probabilistic specification by hyper-parameters that model the cross-category variability in the parameters (Gelman *et al.* 2004). The observation errors, ε , in the $\ln(D)$ estimates were assumed to be normally distributed, giving the model:

$$\ln(D_i) = a_{\text{cat}_i} + b_{\text{cat}_i} A_i + \varepsilon_i \quad \text{Eq. 4.1}$$

where D_i is the cull density on the i th estate and a_{cat} and b_{cat} are the intercept and slope parameters for each landscape category. Note that observation errors are assumed to be constant across landscapes. Immigration rate, v , as fox $\text{km}^{-2}\text{yr}^{-1}$, in each landscape was then obtained by transforming the intercept values:

$$v_{\text{cat}} = e^{a_{\text{cat}}} \quad \text{Eq. 4.2}$$

Vague priors were used for all parameters to minimise any prior influence on the joint posterior and allow predictions from it to reflect the data. The standard deviation in the

normal observation errors was assumed to be uniformly distributed between 0 and 10. The priors for a and b were assumed to be normally distributed with mean (μ_a, μ_b) and standard deviation (σ_a, σ_b) hyperpriors. The mean hyperpriors were assumed to be normally distributed with mean 0 and standard deviation of 1,000, the standard deviation hyperpriors were assumed to be uniformly distributed between 0 and 10. Sensitivity to these prior specifications was tested by varying the standard deviations by one order of magnitude in either direction. The hyperparameters for the intercept were used to describe the posterior predictive distribution for the intercept. Following transformation into real-space, this predictive distribution is suitable for use as an informative prior for immigration rate where landscape type is unknown.

Bayesian analysis was performed using WinBUGS 1.4 (Spiegelhalter *et al.* 2007), implemented from within R using the R2WinBUGS package (Sturtz, Ligges & Gelman 2005). Samples from the joint posterior distribution were obtained using Markov chain Monte Carlo (MCMC) simulation. The posterior was estimated from two chains of 25,000, following an initial burn-in of 50,000 samples. Convergence of the Markov chains to the posterior distribution was diagnosed using the R coda package (Plummer *et al.* 2006). Gelman-Rubin convergence statistics (Gelman *et al.* 2004) were <1.1 for all parameters and Geweke's Z-scores (Geweke 1992) did not fall within the extreme tails of a standard normal distribution, suggesting that the chains had fully converged.

The estimation model assumes a positive relationship between the cull size and area variables. Standardising data on cull size for area effects to account for larger cull sizes on smaller estates can result in spurious correlation when there is no relationship between cull and area, i.e. the cull density ratio variable is inevitably correlated with area (Jackson & Somers 1991). When X and Y are independent variables that are random numbers, standardisation will cause large Y/X values at small values of X, and *vice versa*. This leads to a spurious correlation between Y/X and X. Compared to the situation where a relationship between cull and area exists, the fitting of a regression model to standardised data when there is no relationship between cull and area will therefore result in larger intercepts and more negative slopes due to larger cull density values being found at small areas.

The possibility of spurious correlations influencing the results was examined in two ways. First, the correlation coefficients between cull and area within each landscape were calculated and compared to the correlation coefficients between cull density and area. Second, randomisation testing (Edgington 1995) was used to determine whether the intercept and slope parameter values for each landscape differed significantly from the expected distribution of intercept and slope values from randomised cull and area data. The expected distributions for each landscape were obtained by randomly sampling the cull and area data without replacement to give 9,999 datasets. The cull density was calculated for each dataset and a non-hierarchical version of the model in Eq. 4.1 was then fitted using maximum likelihood estimation. The resulting intercept and slope values were summarised in frequency histograms and compared to the values estimated from the observed data in the same way. Because there was *a priori* expectation that spurious correlation would result in a change in slope and intercept values in one direction, a one-tailed test was applied to determine the statistical significance of the observed data estimates to the randomised distribution.

4.3 Results

4.3.1 NGC data and land categorisation

Compositional analysis found no difference between the landscape composition of estates from using either the known estate boundary or a circular buffer centred on the estate location (Wilks' $\Lambda = 0.705$, $\chi^2_6 = 9.43$, $P = 0.15$, or $P = 0.11$ by randomisation). Circular buffers were therefore used to determine the landscape composition for all estates. The numbers of estates within each landscape category were: arable a ($n = 47$), arable b ($n = 126$), arable c ($n = 37$), pastoral a ($n = 36$), pastoral b ($n = 42$), marginal upland ($n = 92$), upland ($n = 155$). The estates were located throughout both England and Scotland, but few estates were located in Wales (Figure 4.2). Relative to the total area of each landscape category, there were more estates in upland and arable a categories, and fewer estates in the pastoral categories.

4.3.2 Relationships of the fox cull to estate area

Mean annual cull was positively correlated with mean estate area in each landscape, though the correlation coefficient was only weakly positive in arable c, marginal upland and upland (Figure 4.3). The relationships between mean cull density and mean estate area were all negative but the correlations were relatively weak (Figure 4.3). Correlation between $\ln(D)$ and area were generally stronger, providing an additional reason for using a log-linear model. A log-linear model fitted using MLE to the observed data pooled across landscapes was significant ($P < 0.001$) and had an explanatory power of 27.1% (adjusted R^2). Using a log-linear model, randomisation tests indicated the intercept and slope parameter values estimated from the observed data were lower and higher, respectively, than those expected under random association (Figure 4.4). These differences were all significant ($P < 0.05$, one-tailed test).

4.3.3 Immigration rate estimates

Posterior probability distributions for immigration rate in different landscapes were very different, with arable a and b landscapes being significantly higher than marginal upland and upland landscapes (Figure 4.5). Posterior median estimates of annual immigration rate for different landscape categories ranged between 0.87 and 4.06 fox $\text{km}^{-2} \text{yr}^{-1}$ (Table 7.3). Coefficients of variation (CV) ranged from 0.11 to 0.21. Posterior precision was related to the number of estates in each landscape category as posteriors were more precise from those landscapes with data from more estates. The results were not sensitive to alternative prior specifications. The posterior predictive distribution was lognormal with a median of 2.41 fox $\text{km}^{-2} \text{yr}^{-1}$ and a CV of 0.84. The median value was very close to that obtained from the model fitted to pooled data, which was 2.38 fox $\text{km}^{-2} \text{yr}^{-1}$.

4.4 Discussion

This chapter describes a novel method for estimating immigration rate using data from annual fox culling records from managed estates. The expected negative relationships between average annual fox cull per km^2 over the 1996-2000 period and estate area were found in all landscape types. The estimation of immigration rate from these negative

relationships made the assumption that they arose in part because the contribution of immigration to the annual cull increases with decreasing estate size. This is valid because on smaller estates there will be less territory space to support resident foxes and proportionally more boundary relative to area over which immigrant foxes can move. The annual cull on an extremely small estate was thus considered a suitable estimate of the annual rate of immigration onto that estate.

Landscape type had a clear effect on estimated immigration rates of foxes. Immigration rates on estates in arable a and b was four times greater than in upland landscapes. Fox density was proposed as the key determinant of immigration rate at the landscape scale. The pattern in immigration rates onto estates in different landscape types broadly matches the differences in landscape-scale fox density (Figure 4.6) as estimated by faecal density counts (Webbon, Baker & Harris 2004). Upland landscapes had lower estimates of fox density and immigration rate, while arable and pastoral landscapes had higher estimates of both. However, within the arable and pastoral categories the relationship between immigration rate and density was not a perfect match, as immigration rates onto estates in arable a, arable b and pastoral b were higher than expected from fox density alone, and immigration rates onto arable c and pastoral a were lower than expected. The reasons for this are not immediately clear, but are most likely to be due to an interaction between the factors determining fox density – culling and prey availability – and how they may each directly influence immigration rate.

Culling is a determinant of fox density at regional scales (Heydon & Reynolds 2000b). Landscapes are largely regional in their distribution (Figure 4.1) and as culling practices vary between regions (Tapper 1992; Heydon & Reynolds 2000a) it follows that fox density in different landscapes will be affected by variable culling pressure. Similarly, fox density is also determined by prey availability at landscape scales (Webbon, Baker & Harris 2004). Foxes are generalist predators and as such will switch diet to more abundant prey, leading to variation in diet between landscape types (Baker & Harris 2003; Webbon *et al.* 2006). However, the total available prey community differs between landscapes and fox density may partly reflect this. High culling pressures in predator removal experiments have

shown that prey abundance increases in those areas subject to culling (Tapper, Potts & Brockless 1996; Fletcher *et al.* 2010). Correspondingly, fox density has been shown to respond to changes in prey abundance following removal of a key prey species (Angelstam, Lindström & Widén 1984, 1985; Jacquot *et al.* 2013). Culling pressure and prey availability therefore interact to determine fox density, but they are not independent as prey availability is influenced directly by culling of foxes and *vice versa*. If the relationship between culling pressure and prey availability is not linear, then one factor will have more influence on fox density and therefore on immigration rate than the other.

At this point, it must be remembered that the estimates of immigration rate represent values for estates within each landscape, and so factors that influence the source-sink dynamics of the population at this scale become important too. Culling pressure and prey availability are both involved at local scales, but with subtle differences. Culling creates population sinks which foxes may immigrate into (Reynolds, Goddard & Brockless 1993), but it will affect the number of successful immigrants, not the rate of immigration. In contrast, prey availability may directly affect the rate of fox immigration in sink areas of high prey availability as these areas will appear more attractive (i.e. active dispersal, Pulliam 1988). Variation in local scale prey availability might be the reason why fox density fails to convincingly explain immigration rate in lowland landscapes.

Without knowledge of prey availability on these NGC estates, this notion is difficult to explore. Information on prey availability at the estate scale is very scarce with the exception of numbers of all game species shot and numbers of game birds released, which are recorded as part of the NGC. Although fox diet varies both seasonally and between landscapes (Baker & Harris 2003; Webbon *et al.* 2006), game birds from the order Galliformes, including common pheasant (*Phasianus colchicus*), red-legged partridge (*Alectoris rufa*), and grey partridge (*Perdix perdix*) contributed a year-round average of around 16% of fox diet at one location in Britain (Reynolds & Tapper 1995a). The major game bird in Britain is the pheasant, and large numbers (millions) are hand-reared and released annually for sport shooting (Tapper 1992; Aebischer 2013). Hence, estates may create a ‘honeypot’ of higher prey availability for foxes if they annually release high

densities of pheasant, which could result in higher immigration rates. This conclusion is supported by the relationship of the immigration rate estimates obtained using data from NGC estates within the different landscape types to the mean pheasant release densities on these estates (Figure 4.7). The R^2 of this linear regression model was 0.71 and could not be rejected in favour of a multiple-linear model of immigration rate on both pheasant release density and fox density that had an R^2 of 0.68 ($F=0.42$, $P=0.55$). The pheasant releasing data also show that there is variation in mean release density between landscape types, but the standard errors of landscape means indicate there is large variation in release density within landscape types.

The effect of gamekeeper effort also contributes to the larger cull per km² on small estates, and is not independent of the increase from immigration. As estate size increases, the effort of a gamekeeper becomes saturated and is spread more thinly until an additional gamekeeper is clearly needed. Some estates employ several gamekeepers. Information on the number of gamekeepers employed is contributed to the NGC, and in the subset of data used in this analysis the number of gamekeepers' employed does increase with estate area (Figure 4.8). Landscape type appears to be an influence, with arable estates employing more gamekeepers on an estate of a given area compared to upland estates. It might therefore have been appropriate to include gamekeeper numbers as a term in the model to explain some additional variation in fox cull per km². This was not done because the NGC gamekeeper numbers are difficult to interpret as a measure of fox culling effort for the reasons discussed below.

The NGC data include estates with both full- and part-time gamekeepers, with a full-time gamekeeper employed for a whole year entered as a 1.0 and a part-time or amateur gamekeeper as a 0.5 (Tapper 1992). This makes a value of 0.25 a possibility if a part-timer is employed for half the year. These are clearly very subjective values. Quantifying part-time effort is difficult, as part-time gamekeepers cover a full spectrum from those who are very keen and put in similar effort to some full-time gamekeepers, to those who are very time-limited and undertake minimal predator control. The type of shooting estate also affects interpretation, as gamekeepers on estates where game birds are hand-reared for release

generally have considerably less time for predator control compared to those estates aiming to produce wild game, for which predator control is a key ingredient (Tapper 1992; Reynolds & Tapper 1996). Game bird releasing predominantly occurs in lowland arable landscapes and this may explain the higher number of gamekeepers employed in these landscapes.

The results indicate that the standardisation of the fox cull data to remove the effect of area within each landscape type did not result in spurious correlation, and so the modelled patterns between the cull density ratio and area cannot be rejected as purely spurious. The use of ratios for data standardisation is prevalent in ecology, e.g. to remove study area or body size effects from variables of interest (Jackson & Somers 1991). Pearson (1897) documented the problem of spurious correlations in ratio variables over a century ago and, despite several reminders (Kenney 1982; Jackson & Somers 1991; Brett 2004), it is still not widely appreciated and can be the cause of erroneous conclusions. An example of this is in fisheries science and the estimation of the Ricker stock-recruit population dynamics model using data on the numbers of recruits R and spawners S . It is common to estimate the parameters of this model by regressing $\ln(R/S)$ against S . This is despite a warning by Walters and Martell (2004 p. 160) about the use of $\ln(R/S)$ information in the analysis of compensatory change when R and S have not been measured accurately. Moreover, as there exists no evidence of studies testing for spurious correlation prior to analysis, potentially some of the estimates of stock reference points could be erroneous. Had there been no relationship between cull and area in these NGC data, performing the analysis would have resulted in estimates of immigration rate that were artificially high. Evaluation of the results from use of ratios using randomisation testing is therefore an important step in ensuring that conclusions are not erroneous (Jackson & Somers 1991).

This approach to estimation of immigration rate is a valuable alternative to using expensive tagging-based field methods. The use of a Bayesian hierarchical modelling framework for the analysis allows the posterior predictive distribution for immigration rate to be determined, a distribution that is potentially very useful when used as an informative prior probability distribution in population dynamics models where immigration is a key process. Construction of this prior made the assumption that net local production would be zero on

extremely small estates. There was potential for positive bias in the estimate of immigration rate if there was any local production, but this bias was not expected to be large. In any case, as the posterior predictive distribution was relatively imprecise ($CV > 0.8$) it was expected that when used as an informative prior within a population dynamics model the posterior for immigration rate would be updated from this prior by the data used to fit the model.

4.5 Tables

Table 4.1. Summary statistics from the posterior probability distributions of immigration rate in different landscapes and the posterior predictive distribution. Median values and credible intervals are all in fox $\text{km}^{-2}\text{yr}^{-1}$.

Landscape	Median	CV	95% C.I.	
			lower	upper
arable a	4.06	0.17	2.88	5.71
arable b	3.85	0.11	3.11	4.75
arable c	2.54	0.21	1.75	3.90
pastural a	2.76	0.18	1.94	3.99
pastural b	2.94	0.18	2.07	4.18
marginal upland	1.80	0.14	1.37	2.36
upland	0.87	0.12	0.69	1.10
posterior predictive	2.41	0.84	0.43	12.78

4.6 Figures

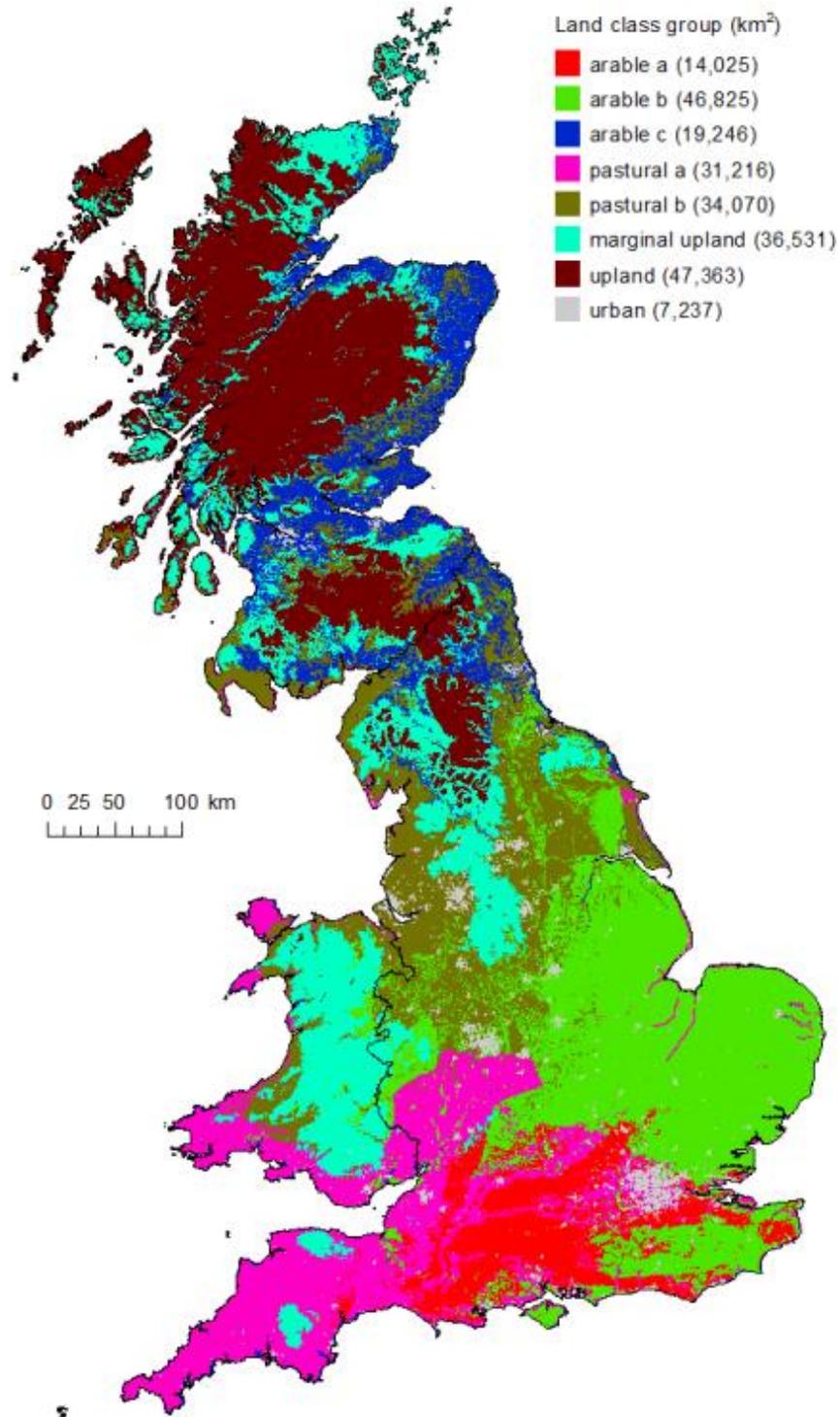


Figure 4.1. Map of Britain (England, Scotland & Wales) showing landscape categories obtained from grouping the 40 land classes surveyed in Countryside Survey 2000 (following original grouping in Bunce *et al.* 1996a; Walsh & Harris 1996).

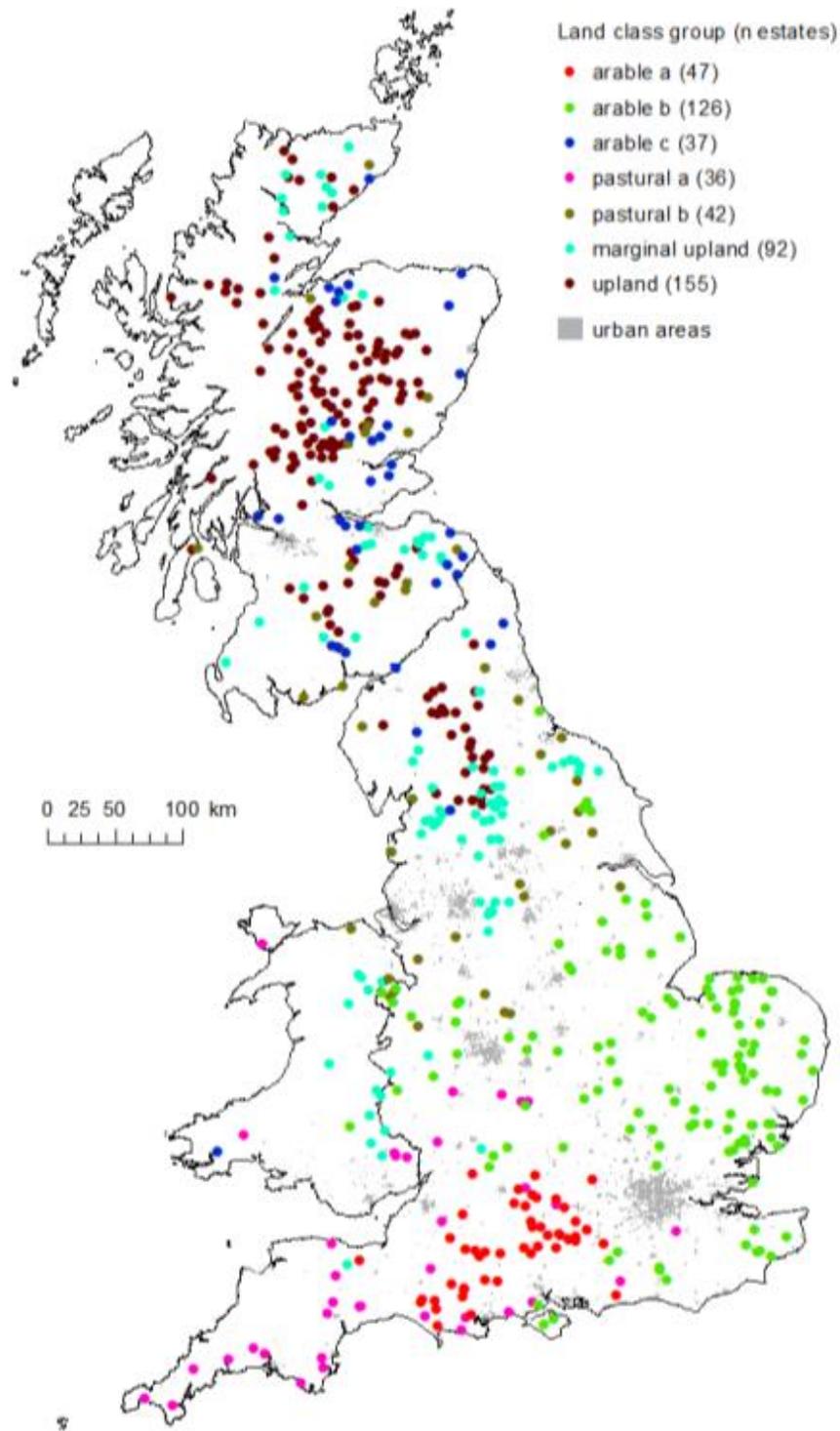


Figure 4.2. Location and landscape category of 535 British shooting estates that contributed data on foxes culled to the National Gamebag Census (NGC) between 1996 and 2000.

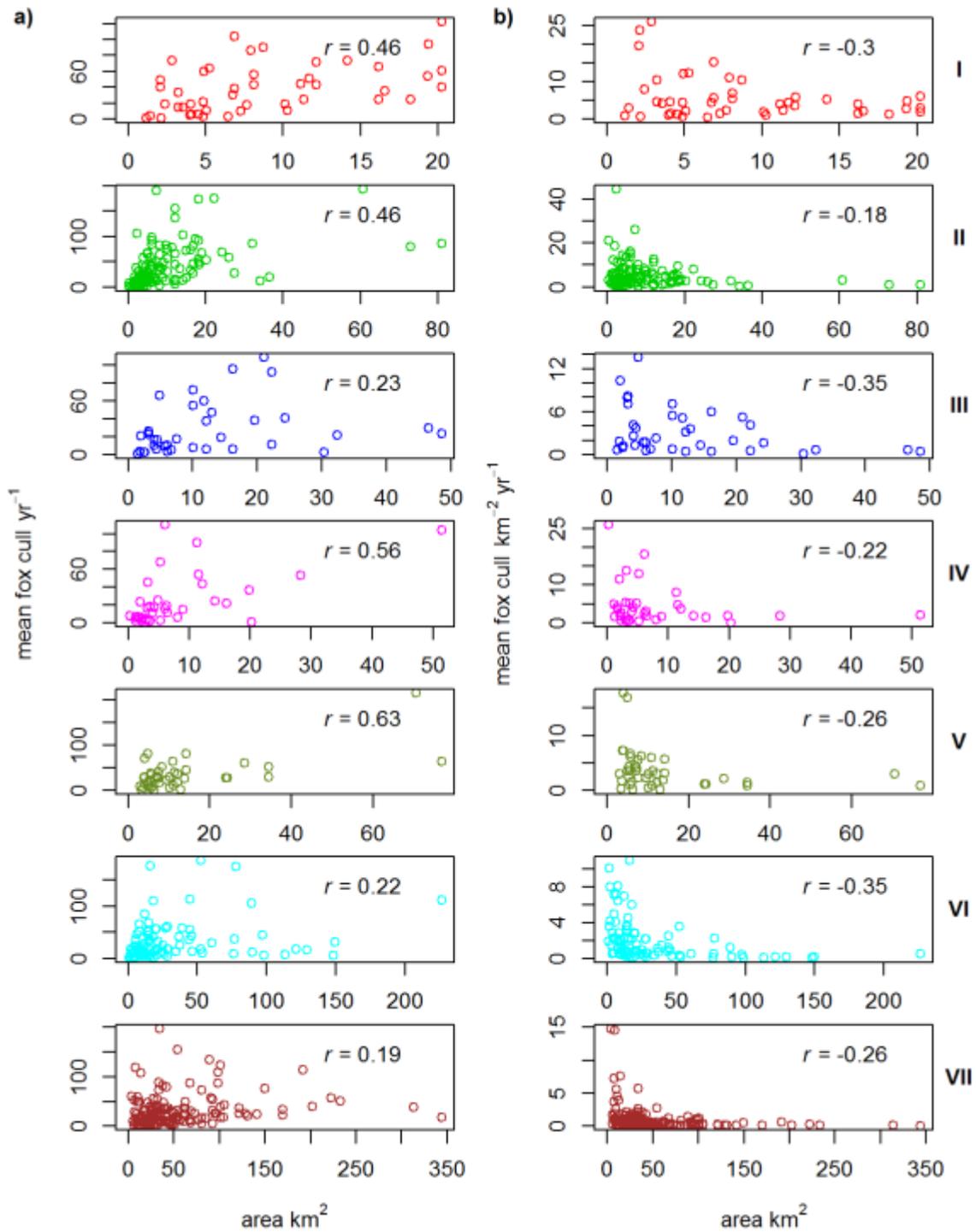


Figure 4.3. Relationships between a) mean annual cull and estate area, and b) mean annual cull density and estate area within each landscape category. The Pearson correlation coefficient is displayed on each panel. The numeral on the right of each row corresponds to the landscape category (I = arable a, II = arable b, III = arable c, IV = pastural a, V = pastural b, VI = marginal upland, VII = upland).

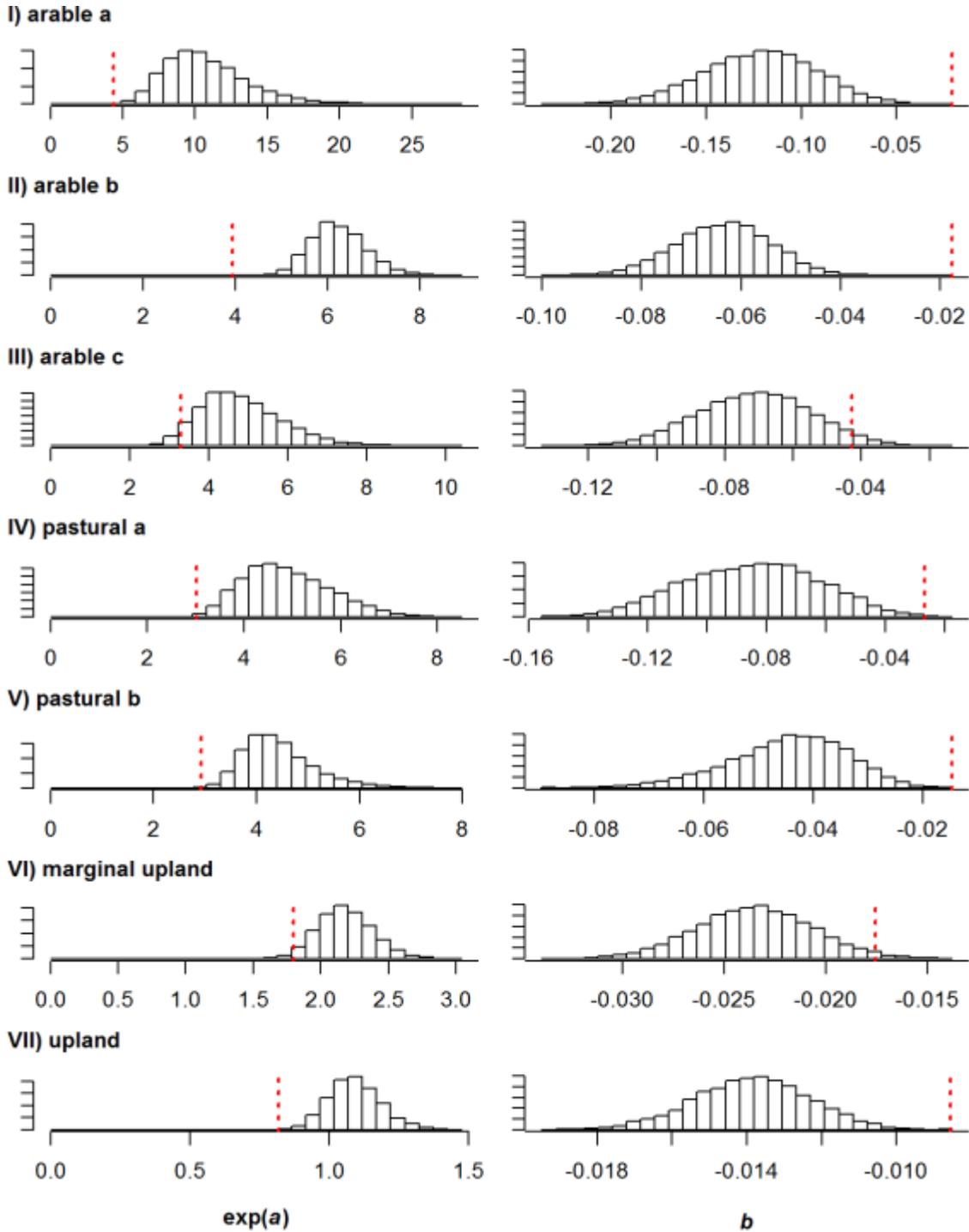


Figure 4.4. Frequency histograms for each landscape category showing 10,000 intercept ($\exp(a)$) and slope (b) estimates from a randomisation test of the cull density and area relationship. Locations of the empirically estimated values are shown by the dashed red lines. The y-axes are not labelled for clarity.

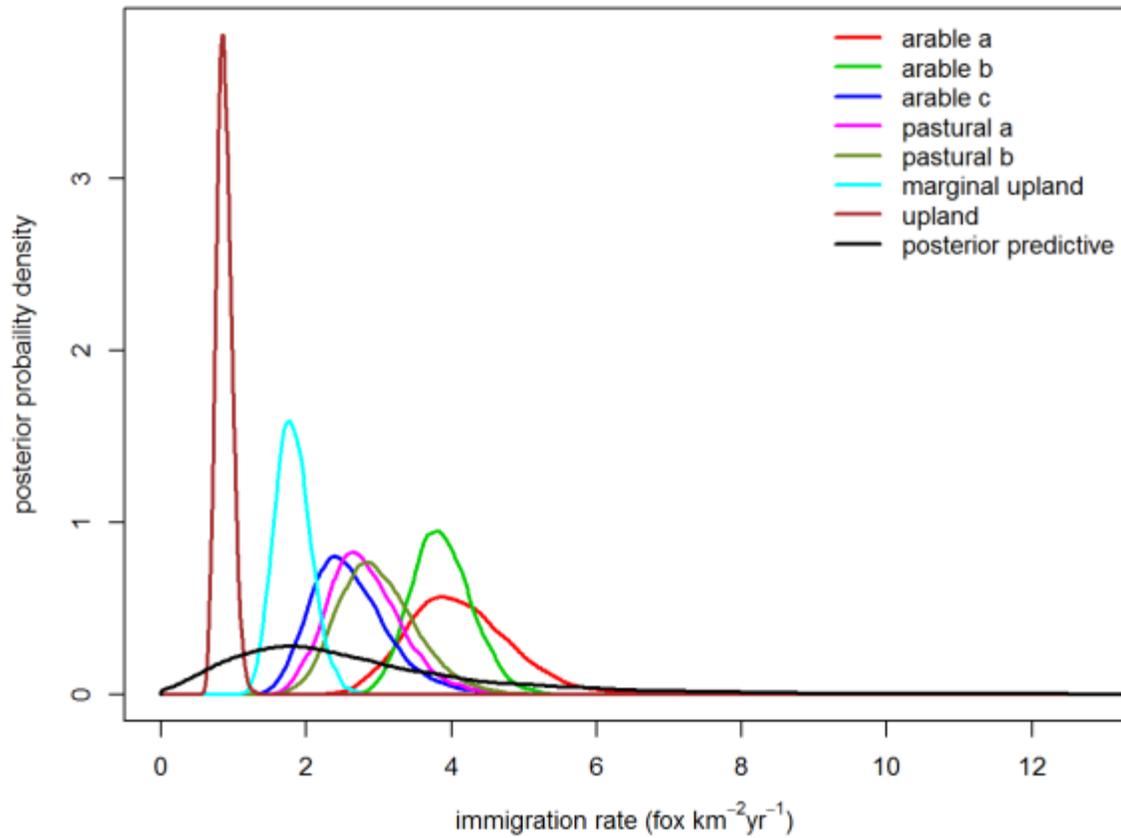


Figure 4.5. Posterior probability density functions for immigration rate in each landscape category. The posterior predictive density function was determined by the hyper-parameters of the hierarchical model.

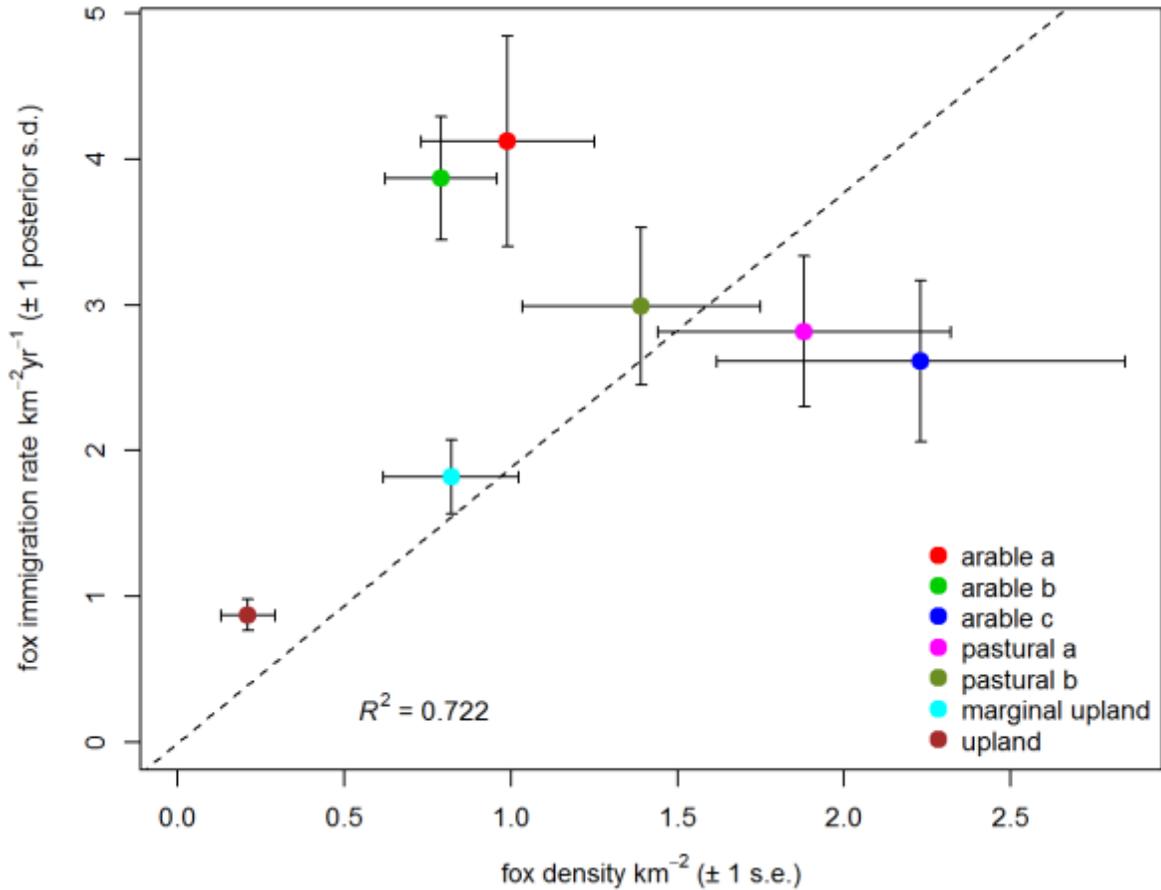


Figure 4.6. Relationship between posterior estimates of immigration rate in each landscape category with fox density estimated from faecal surveys along linear features in these landscapes (Webbon, Baker & Harris 2004). Dashed line shows the fit of a linear model with the intercept fixed at zero to account for the assumption that immigration onto estates within a landscape cannot occur without foxes being present in the surrounding region.

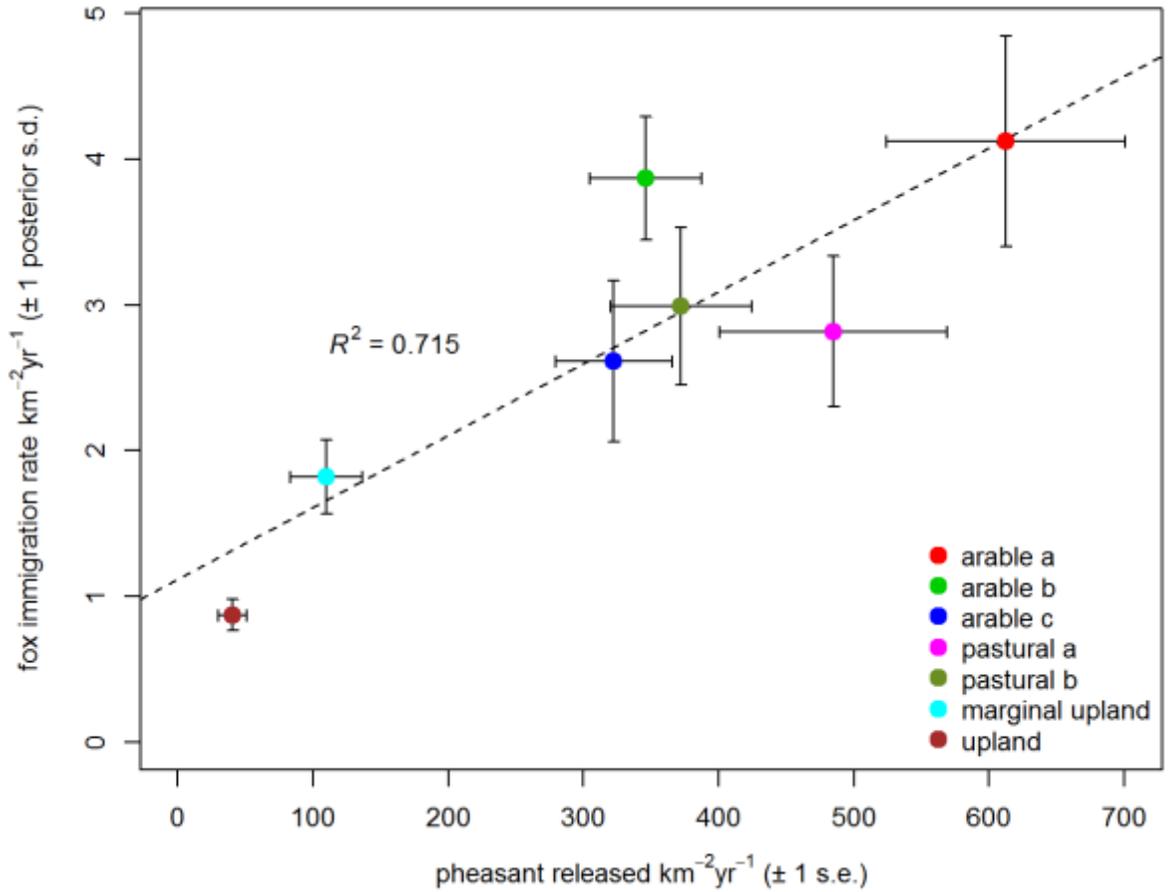


Figure 4.7. Relationship of estimated immigration rate to the mean density of pheasant released annually onto estates within each landscape. Data were obtained from the National Gamebag Census from 535 estates controlling foxes during the period 1996-2000. Dashed line shows the fit of a linear model.

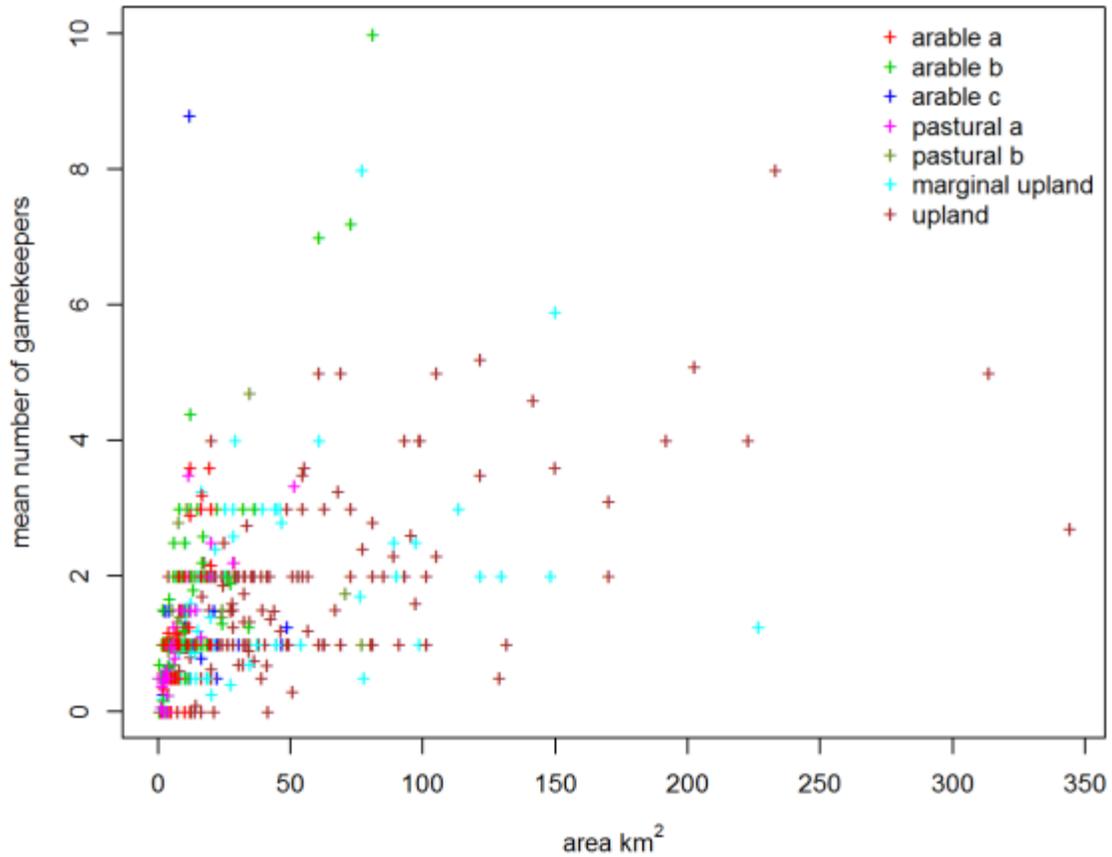


Figure 4.8. Relationship between the mean number of gamekeepers employed annually and estate area in each landscape category from those NGC estates contributing data on fox bags for the period 1996-2000.

Chapter 5: Meta-analytic methods to establish informative Bayesian priors for fox non-culling mortality rate

5.1 Introduction

Animals are killed by competing mortality risk factors that must each be accounted for in population dynamics models. Models for harvested or controlled species, such as that developed for red foxes *Vulpes vulpes* in Chapter 3, are often conditioned on catch or cull data, meaning these are assumed to be correct measures of the deliberate removals from the population by harvest or control. Mortality can also be caused by non-anthropogenic factors, e.g., disease, and by non-deliberate anthropogenic factors, e.g., road traffic collisions (RTC). To account for these additional mortality factors, many population dynamics models include an additional parameter for the instantaneous rate of natural mortality M . In this Chapter, the term “natural mortality” will be considered to include both non-anthropogenic and also non-deliberate anthropogenic mortality on foxes, i.e. non-culling mortality.

Rates of natural mortality are determined by intrinsic or extrinsic mortality factors that result in death before the maximum possible life span (McCoy & Gillooly 2008). Intrinsic factors are linked to the resource allocation choices an individual makes and are therefore determined by metabolic rate (Brown *et al.* 2004); animals with higher metabolic rates can reproduce faster but incur higher rates of cell damage or decay that result in senescence, perhaps due to the accumulation of oxidative free radicals which are by-products of metabolism (Hulbert *et al.* 2007; McCoy & Gillooly 2008). Extrinsic factors include disease, predation, starvation, accidents or inclement weather that are capable of causing death at any age (Ricklefs 2010a). When included in population dynamics models, it is usually assumed that M represents the combined mortality risk from both of these types of mortality factor.

It is typically difficult to estimate M within a population dynamics model due to confounding with other parameters (Chapter 3), and instead it is often assumed to be a constant and fixed at a best-guess value to avoid estimating it (McAllister *et al.* 2004; Robert

et al. 2010). However, inference from population dynamics models has proven to be sensitive to changes in M of 0.1 yr^{-1} or less (Clark 1999), so fixing M at a point estimate will generally underestimate the uncertainty associated with model results and this can have major effects on subsequent management recommendations. A Bayesian approach that allows estimation of M , rather than having to fix it, and that incorporates parameter uncertainty in such situations is therefore preferable (Hilborn & Liermann 1998). The use of informative prior probability distributions that bound the parameter space of M to biologically realistic values for a particular species' population can improve inference from population dynamics models, particularly in conditions where the data used to fit a model are sparse and noisy.

Natural mortality in populations of most animal species, particularly of carnivores, is extremely difficult and expensive to estimate directly; studies typically require large samples of detailed telemetry and tagging data that can be used in mark-recapture models (e.g. White & Burnham 1999; Whitlock, McAllister & Block 2012). Such models become further complicated when there are concurrent removals from the population (Pollock, Conroy & Hearn 1995; Toigo *et al.* 2008). Therefore, M is often unknown and in absence of such tagging data it must be estimated by other, indirect methods. Most of these methods arose in a fisheries context because M is one of the most influential quantities in fisheries stock assessment and management (Vetter 1988). Some of these methods directly estimate M while others estimate total mortality rate (Z), which approximates M if the studied population has suffered only minimal anthropogenic impacts on survival, e.g., harvesting or culling, habitat loss, or competition from invasive species.

The indirect methods for estimating mortality rate include 1) catch-curve analysis using catch-at-age data (Ricker 1975; Deriso, Quinn & Neal 1985); 2) multispecies approaches (e.g. multispecies virtual population analysis and cohort analysis) that estimate the contribution of predation mortality to Z (Pope & Knights 1982; Gislason & Helgason 1985); and 3) use of predictive equations, derived from meta-analyses across diverse taxonomic groups, describing the relationship between mortality rate and life history attributes, such as von Bertalanffy growth parameters (Pauly 1980; Ralston 1987) or

longevity (Hoenig 1983), or the allometric relationship between mortality rate and body mass (Lorenzen 1996; Savage *et al.* 2004a; McCoy & Gillooly 2008). Methods 1) and 2) require detailed knowledge on the age structure of animals removed from the population, which for harvested or controlled populations will not necessarily be a representative sample. In addition, for controlled fox populations, e.g. in Britain, these data are typically not recorded and would be expensive to obtain. Therefore, in the absence of detailed tagging studies, life history and allometric relationships are the only option for estimating M and establishing a Bayesian informative prior.

Life history attributes describe the events that relate to the life history of an animal, and include age at maturity, maximum intrinsic rate of population growth, adult instantaneous natural mortality rate and longevity. Between different species these attributes show variation that reflects the wide range of life history strategies that exist in nature, but despite this variation many relationships between attributes are invariant across a diverse array of species (Charnov 1993). For example, invariant allometric relationships based upon power scaling functions of adult body mass are well studied and have been used to predict life history attributes for many different taxonomic groups, e.g. invertebrates, fish, birds, and mammals (Peters 1983; Calder 1984; Charnov 1993). Such allometric scaling relationships can also predict physiological and size variables (Calder 1984). Given knowledge about resource supply rates they can further predict population interactions such as carrying capacity and rates of competition and predation, and ecosystem interactions such as rates of biomass production and patterns of trophic dynamics (Brown *et al.* 2004).

Physiological theory based upon how metabolism varies with body size and temperature can explain allometric relationships (West, Brown & Enquist 1997; Brown *et al.* 2004; Savage *et al.* 2004a). Metabolic rate determines the rate of energy uptake and its allocation to processes such as growth, survival and reproduction, and is itself limited by the rate at which an organism can transport materials around its body (Brown *et al.* 2004). This means that the metabolic rate of a species is largely determined by its body size (with environmental temperature being an important additional factor for ectotherms). Metabolic rate can be predicted by an allometric equation (Huxley 1932) of the form:

$$Y = Y_0 W^b \quad \text{Eq. 5.1}$$

where Y is metabolic rate of the entire organism, W is body mass, Y_0 is a normalisation constant and b is an allometric scaling exponent. There is considerable debate over whether the metabolic rate scaling exponent is equal to $\frac{2}{3}$ or $\frac{3}{4}$ (West, Brown & Enquist 1997; Dodds, Rothman & Weitz 2001; West & Brown 2005; White & Seymour 2005; Savage *et al.* 2007; Hudson, Isaac & Reuman 2013). For most biological parameters, the allometric scaling exponents are found to be multiples of $\frac{1}{4}$ powers of body mass (Savage *et al.* 2004b), rather than the $\frac{1}{3}$ powers that would be expected from geometric scaling, i.e., derived by considering the surface area-to-volume ratio (Dodds, Rothman & Weitz 2001). Allometric theory uses this body mass-metabolic rate scaling relationship to predict other quarter power scaling body mass relationships, such as life history attributes (Savage *et al.* 2004a). Rates such as r and M are greater for small-bodied species than for large-bodied species, and the allometric scaling exponent for these relationships has been shown empirically to equal -0.25 (Savage *et al.* 2004a; McCoy & Gillooly 2008).

The utility of allometric scaling in establishing Bayesian prior probability distributions for annual survival rate in birds and mammals was recently proposed by McCarthy *et al.* (2008), who compiled a database of adult mammal survival rate estimates but excluded studies of populations that had obviously suffered from anthropogenic impacts. The estimated survival rates were then assumed to be close to the actual natural survival rates for these populations. Using the allometric relationship between M and body mass (W), and assuming that M is constant over a time interval of length t , the probability s of surviving this interval is:

$$s(t) = e^{-Mt} = e^{-aW^b t} \quad \text{Eq. 5.2}$$

Rearranging led McCarthy *et al.* (2008) to a linear relationship between the complementary log-log transformed survival rate ($\ln\{-\ln[s(t)]\} - \ln[t]$) and $\ln(W)$, where a became the intercept term and b became the slope of the relationship, which is equal to the scaling exponent. Using a Bayesian mixed effects model that accounted for taxonomic group and study effects, McCarthy *et al.* (2008) showed that b was close to the -0.25 value predicted

from metabolic theory (Brown *et al.* 2004; Savage *et al.* 2004b), though the alternative -0.33 value predicted by geometric scaling (Dodds, Rothman & Weitz 2001) could not be discounted as the 95% credible interval was $[-0.34, -0.15]$. The parameter estimates from the model were used to generate posterior predictions of survival rate for species of given body mass that could be used in future studies as priors, allowing the application of this approach using the mammalian data and appropriate random effects to establish a prior for fox M .

In addition to allometric relationships, similar relationships exist between other life history attributes, e.g., adult longevity and age at maturity. Studies on life history invariant relationships (e.g. Charnov 1993) have produced a number of empirical equations that use one variable to predict another, such as mortality rate. It is intuitive that animals from a population with a low mortality rate would be expected to live longer than those from a population with a high mortality rate. This inverse relationship between mortality rate and longevity was described by Hoenig (1983). Assuming that total instantaneous adult mortality rate Z is constant and does not vary with age, the proportion of a population N surviving to age t (i.e. N_t/N_0) is equal to e^{-Zt} . If longevity in a population is defined as the age, t_L , to which a proportion, k , of the animals survive, then:

$$k = e^{-Zt_L} \tag{Eq. 5.3}$$

where k is some small constant, e.g., 1% (Hoenig 1983). This equation describes a hyperbola across the range of Z and t_L that can be linearised by plotting $\ln(Z)$ against $\ln(t_L)$ to produce an inverse relationship between Z and t_L . The slope of this relationship should be -1 if the assumptions of minimal survivorship after age t_L and constant Z hold.

It is difficult to determine t_L directly without censusing the entire population, but it is easier to find the maximum age, t_{\max} , from a sample of animals. Several comparative studies on aquatic taxa suggested that the inverse linear relationship between longevity and Z holds if t_{\max} is substituted for t_L (e.g. Beverton 1963; Ohsumi 1979; Hoenig 1983). By making the assumption that t_{\max} is a suitable substitute for t_L it is possible to predict Z for a species in a

given taxonomic group from the maximum age observed in a sample of a population using predictive regression equations of the form

$$\ln(Z) = a + b \ln(t_{\max}) \quad \text{Eq. 5.4}$$

where a and b are intercept and slope parameters (Hoenig 1983). Data compiled on total adult mortality rates (estimated using catch-curve analyses that assume constant Z) and maximum age from unexploited or lightly exploited populations of cetaceans, fish and molluscs showed similar relationships between taxonomic groups (Hoenig 1982). A regression equation fit to the pooled data had a high coefficient of determination (0.82) and slope and intercept parameter estimates of -0.982 and 1.44 , respectively (Hoenig 1983). Given that the estimated slope was close to the -1 value predicted from theory, it is reasonable to assume that the approach has potential application to other taxonomic groups. For example, the analysis could be used to form a predictive equation for species from the order Carnivora that would enable fox Z prediction from an estimate of maximum age.

Although the Hoenig (1983) model based upon t_{\max} has been shown to be among the most reliable of the life history-based mortality rate estimation approaches (Hall, Hesp & Potter 2004; Kenchington 2014; Then *et al.* 2014) a weakness was that it did not take sample size into account. It thereby only gave a point estimate for Z without any assessment of estimate precision. Some methods of obtaining confidence limits have been suggested, depending on whether information on the sample size of aged animals used to estimate maximum age is available. Without sample size information, the Hoenig (1983) model can be refitted to the data (i.e. Hoenig 1982) to obtain the mean and standard error of the independent variable, maximum age. It is then assumed that the predicted $\ln(Z)$ values have a Student's t distribution (Hall, Hesp & Potter 2004). If sample size is available, then the likelihood function of Z associated with the maximum age from the sample can be approximated by a simulation approach (Hall, Hesp & Potter 2004). An alternative approach to assessing the precision in Z estimates is to refit the Hoenig (1983) model using a Bayesian formulation that would incorporate uncertainty in the regression parameter estimates and result in a predictive posterior probability distribution for Z . Applying a Bayesian approach

would also enable a prior probability distribution for fox Z to be established if data on the order Carnivora were incorporated.

The aims of this chapter are to establish a prior probability distribution for instantaneous mortality rate of British foxes using two different meta-analyses based upon: 1) the allometric relationship between instantaneous mortality rate and body mass (McCarthy, Citroen & McCall 2008), and 2) the life-history relationship between instantaneous mortality rate and longevity (Hoenig 1983). The effect of the constant mortality rate-over-age assumption was examined under different simulated scenarios of senescence to assess bias in both the data used to fit the models and the estimates from the Hoenig model. The median mortality rate estimates from both models were used to construct survivorship-at-age curves for comparison with those available for culled fox populations from different regions across Britain.

5.2 Methods

5.2.1 McCarthy model

The original database (McCarthy, Citroen & McCall 2008) contained few studies on small carnivores, despite this order being the most diverse in body mass, and it did not contain any estimates from the family Canidae. To allow a prior for fox M to be more reliably established using this approach, the database needed improved coverage of the order Carnivora. The survival estimate database for Carnivora was updated to include any suitable estimates of mean adult survival (i.e. studies that reported estimate precision and met the minimal anthropogenic impact criteria) that were overlooked by McCarthy *et al.* (2008) or were published during the intervening period. For studies where the estimated precision was described by a 95% confidence interval instead of an SE, the SE was calculated as the range of the 95% CI divided by 4 given that the 95% CIs were approximately symmetrical (McCarthy, Citroen & McCall 2008).

Body masses for each species were taken from the reporting study if possible, but following McCarthy *et al.* (2008) if mean body mass for the study population was not

reported it was taken from the location closest to or most geographically similar to the location of the study from either Silva and Downing (1995) or Smith *et al.* (2003). This resulted in 18 additional survival estimates for Carnivora, from Canidae ($n = 6$), Mustelidae ($n = 6$), Felidae ($n = 5$), and Herpestidae ($n = 1$). The updated database contained data for 61 species, across 12 orders, and from 56 studies (Figure 5.1). There are large inter-order differences in mortality rate (Figure 5.2) and as a result taxonomic order exhibited the greatest level of variation in the random effects (McCarthy, Citroen & McCall 2008). Within the order Carnivora, there were data for 20 species, across eight families, and from 23 studies (Figure 5.3). Variation in survival rate existed both between and within carnivore families; this variation was not explicitly modelled but was accounted for by the random effect for species.

Annual survival rate estimates were modelled using a beta distribution, which is defined on the appropriate $[0, 1]$ interval and has parameters α and β . The estimation error of each survival estimate was considered in the parameterisation of the beta distribution by using the effective sample size on which each estimate was based. From the standard error of a proportion based on binomial sampling, the effective sample size n is determined as:

$$n_i = s_i(1 - s_i)/SE_i^2 \quad \text{Eq. 5.5}$$

where s_i is the i th survival rate estimate and SE_i is its standard error (McCarthy, Citroen & McCall 2008). The parameters of the beta distribution for each estimate are then given by:

$$\alpha_i = s_i(n_i - 1) \quad \text{Eq. 5.6}$$

$$\beta_i = (1 - s_i)(n_i - 1) \quad \text{Eq. 5.7}$$

(Kendall 1998).

Though most studies estimated an annual survival rate, the McCarthy *et al.* (2008) model explicitly incorporated time, as a portion of a year, to account for studies where survival rate was estimated over shorter time intervals (e.g. monthly or seasonal survival). McCarthy *et al.* (2008) also recognised that the error term in the model must account for

possible dependence among the survival estimates (e.g. due to being obtained from the same study or were for taxonomically related species). Including random effects for order (θ_{order}), species (ζ_{species}), study (η_{study}), and individual estimates within studies (e.g. estimates for different years, ages, or classes of individuals, ε) gave the Bayesian mixed effects model of McCarthy *et al.* (2008):

$$\ln[-\ln(s_i)] = \ln(a) + b \ln(W_i) + \ln(t) + \theta_{\text{order}_i} + \zeta_{\text{species}_i} + \eta_{\text{study}_i} + \varepsilon_i \quad \text{Eq. 5.8}$$

Ideally, the taxonomic structure would be explicitly incorporated into the model (with the random effects nested as order > species > study), but this was not possible due to the crossover between levels caused by there being studies that contained survival estimates for multiple species within >1 order. Here, a similarly structured Bayesian mixed effects model was used to establish a prior for the instantaneous natural mortality rate of foxes by transforming the posterior predictions of annual survival rate to instantaneous mortality rates within the model ($M = -\ln(s)/t$).

Bayesian analysis was performed using WinBUGS (Spiegelhalter *et al.* 2007), implemented from within the R statistical software (R Core Team 2013) using the R2WinBUGS package (Sturtz, Ligges & Gelman 2005). The body mass data were mean-centred to reduce correlation between the fixed effects (a , b) and improve sampling efficiency. Similar to McCarthy *et al.* (2008), non-informative priors were used for the parameters to minimise any prior influence on the posterior and allow predictions from it to reflect the data. The priors for the a and b parameters were assumed to be normally distributed with a mean of 0 and a standard deviation of 1,000 (equivalent to a precision of 1×10^{-6}). The priors for the random effects for order, species, study and individual estimates (θ , ζ , η , ε) were assumed to be normally distributed with a mean of 0 and standard deviations of ν , φ , ρ , σ respectively. The random effect standard deviation hyperpriors (ν , φ , ρ , σ) were assumed to be uniformly distributed between 0 and 10.

The model was used to predict annual survival rate and instantaneous mortality rate for species across the range of Carnivora body masses, given that transformation of $s(t)$ yields $M = -\ln(s)$ where $t = 1$ year. M for British foxes was predicted based on the mean

body mass of 6.5 kg from the FMS data (see Chapter 2), with the addition of the random effect for the Carnivora order.

Samples of the posterior distribution of the parameters were obtained using Markov chain Monte Carlo (MCMC) methods, with an initial burn-in of 250,000. Some parameters showed strong autocorrelation, so to reduce this every hundredth sample was recorded and the posterior distribution was estimated from 50,000 samples. Convergence of these samples to the posterior distribution was assessed using the R CODA package (Plummer *et al.* 2006) by examination of two independent Markov chains and calculating the Gelman-Rubin convergence diagnostic (Gelman *et al.* 2004). When this value became <1.01 , the chains were assumed to have converged.

The posterior distribution for predicted fox instantaneous mortality rate was then used to establish a prior probability distribution by using it to parameterise a suitable candidate distribution, i.e. one defined on the $[0, \infty]$ interval. The lognormal, gamma and generalised gamma distributions were considered, and the parameters of these distributions were estimated using maximum likelihood estimation (MLE). The choice of distribution was based upon both visual fit to the posterior probability density function (PDF) and using the Kolmogorov-Smirnov goodness-of-fit (GOF) test to the posterior cumulative distribution function (CDF). In view of the large number of posterior samples, and because the expected frequencies of tested distributions did not come from sample data but from posterior parameter estimates, a large sample extrinsic hypothesis Kolmogorov-Smirnov GOF test was used (Sokal & Rohlf 1995).

5.2.2 Hoenig model

The Bayesian formulation of the Hoenig (1983) model developed here permits group-level parameter estimation from the pooled dataset and includes an estimation error term (ε) for the unexplained variation attributed to each Z estimate. The Z estimates were assumed to follow a lognormal distribution, so ε are the deviates in $\ln(Z)$. The slope and intercept parameters are estimated for each group as random effects in the model:

$$\ln(Z_i) = a_{\text{group}_i} + b_{\text{group}_i} \ln(t_{\text{max}_i}) + \varepsilon_i \quad \text{Eq. 5.9}$$

where Z_i is the i th mortality rate estimate. The above model makes the assumption that ε does not differ between taxonomic groups; however, this is probably unrealistic due to the differing sampling methods used for each group. To account for the likelihood of estimation error differing between taxonomic groups, an alternative model included additional parameters for the estimation error within each group ($\varepsilon_{\text{group}}$). The suitability of using pooled ε was assessed by examining posterior probability distributions for differences between $\varepsilon_{\text{group}}$ and by comparing the Deviance Information Criterion (DIC; Spiegelhalter *et al.* 2002) for each model.

The above model has a non-hierarchical structure that assumes independence in parameters between taxonomic groups. However, given both the theory behind the model and the data it is reasonable to assume that the regression parameters from different groups are related to each other; that is, each group has a unique value for a given parameter but these parameter values come from a common population distribution shared among groups. Assuming each group is exchangeable into this cross-group distribution, this structure can be modelled using a Bayesian hierarchical model where the group parameters are given a probabilistic specification by hyper-parameters that model the cross-group variability in parameters (Gelman *et al.* 2004). The use of a hierarchical model also results in more efficient inference for regression parameters than using either complete or no pooling, typically resulting in more accurate estimation of variation between groups (Gelman & Hill 2007). As a comparison of the structures, the results from both a non-hierarchical and hierarchical parameterisation of the Hoenig (1983) model are presented here.

The Hoenig (1982) database on cetaceans, fish and molluscs did not contain any data on carnivores, so this was updated to include estimates of instantaneous mortality rate (or annual survival rate that could be transformed to Z) for carnivore species. As the sampling precision of each Z estimate in the Hoenig (1982) data was unknown (no information on SE or confidence intervals were available) this information was not included for carnivores and not incorporated into the model. Only studies that were noted to not have suffered from

anthropogenic disturbances and which information on the maximum age could be obtained were included. Maximum age was taken from the reporting study if possible, but if the maximum age of the study population was not reported it was taken from the location closest to or most geographically similar to the location of the study. The updated database contained 165 Z estimates across 90 species in four taxonomic groups, and from 92 studies (Figure 5.4). Within the carnivore group there were 31 Z estimates across 14 species in the Canidae ($n = 3$), Felidae ($n = 7$), Mustelidae ($n = 7$), Phocidae ($n = 6$), Procyonidae ($n = 2$), and Ursidae ($n = 6$) families (Figure 5.5). Nesting structure was not considered within this model because the data from each group were not at comparable taxonomic levels (Carnivora and Cetacea being orders, Mollusca being a phylum, and fish being paraphyletic).

Bayesian analysis was performed using WinBUGS (Spiegelhalter *et al.* 2007), implemented from within the R statistical software (R Core Team 2013) using the R2WinBUGS package (Sturtz, Ligges & Gelman 2005). The maximum age data were mean centred to reduce correlation between the random effects (a , b) and improve sampling efficiency. Non-informative priors were used for all parameters to minimise any prior influence on the posterior and allow predictions from it to reflect the data. Given that the Z estimates come from a lognormal distribution, the priors for the standard deviation in the deviates of $\ln(Z)$ were assumed to be uniformly distributed between 0 and 10. In the non-hierarchical model, the priors for a , and b were assumed to be normally distributed with a mean of 0 and a standard deviation of 1,000. In the hierarchical model, the priors for a and b were assumed to be normally distributed with mean (μ_a, μ_b) and standard deviation (σ_a, σ_b) hyperpriors. The mean hyperpriors were assumed to be normally distributed with mean 0 and standard deviation of 1,000, the standard deviation hyperpriors were assumed to be uniformly distributed between 0 and 10.

The model was used to predict instantaneous mortality rate for species across the maximum age range of the order Carnivora as well as for British foxes. Estimates of the maximum age of wild rural British fox populations show regional variation from age six to nine (Baker & Harris 2008). While this may reflect regional variation in culling effort, causing lower maximum age estimates in regions with more intensive culling and vice versa

(Lloyd 1980; Heydon & Reynolds 2000b), it also reflects the sample size of aged foxes as the nine year-old foxes were found in the largest sample ($n=405$, Kolb & Hewson 1980). Survivorship curves from these regional data follow a pattern of approximately 75% mortality in the juvenile year, followed by approximately 50% mortality in each subsequent adult year, suggesting that only 1 in 1,000 foxes will survive to age nine (cf. Macdonald & Reynolds 2004), and that large sample sizes will be necessary to detect the oldest foxes reliably. A maximum age of nine is supported by data from elsewhere, e.g. Europe (Mulder 2004). Z for British foxes was therefore estimated from the model using a maximum age of nine. The potential bias in the Z estimate from use of an incorrect age was examined by calculating the percent relative bias:

$$\text{PRB} = (Z_9 - Z_{\text{age}})/Z_{\text{age}} \quad \text{Eq. 5.10}$$

where Z_{age} is the estimated Z for a given maximum age.

Samples of the posterior distribution of the parameters were obtained using Markov chain Monte Carlo (MCMC) methods, with an initial burn-in of 100,000. Some parameters showed strong autocorrelation, so to reduce this every hundredth sample was recorded and the posterior distribution was estimated from 50,000 samples. Convergence of these samples to the posterior distribution was assessed using the CODA package (Plummer *et al.* 2006) in R by examination of two independent Markov chains and calculating the Gelman-Rubin convergence diagnostic (Gelman *et al.* 2004). When this value became <1.01 , the chains were assumed to have converged.

5.2.3 Mortality rate-at-age assumption bias

The assumption that mortality rate is constant across adult age classes is made in both deriving the Hoenig (1983) model and in estimating adult Z using catch-curve analysis, the method used to obtain the mortality rate estimates for the original Hoenig (1982) dataset. It was also an implicit assumption in the mammalian mortality rate estimates from studies used in both models, which used either mark-recapture models (Lebreton *et al.* 1992; White & Burnham 1999) or Kaplan-Meier survival analysis (Pollock *et al.* 1989) to estimate annual

mortality rate. While these methods can estimate age-specific mortality rates, the adult age classes were most frequently pooled before analysis due to small sample sizes in the older age classes, resulting in one adult mortality rate estimate. In populations where senescence causes an increase in mortality rate with age the constant mortality assumption is violated. In such populations that mortality rate estimates in the data will be negatively-biased as they will not account for the mean mortality rate as calculated across ages being higher due to the increased mortality rate in older age classes. This potential bias was examined with respect to 1) the mortality rate data used in both models, and 2) the estimated Z from the Hoenig model, given that the maximum age data in a population experiencing senescence will be lower than one in which mortality rate is constant over age.

The bias in the mortality rate data was examined by comparing mean mortality rate across ages obtained from a simulation model of age-specific mortality rates to the constant Z as estimated by a catch-curve analysis performed on the numbers-at-age that were predicted by the simulation model. Three different ageing models were used to describe how instantaneous mortality rate-at-age (M_x) increased with age (x), assuming that the onset of senescence begins after the age-at-maturity (i.e. adult age class zero) is reached:

- 1) Constant model. Mortality rate reflects only the extrinsic mortality rate (M_0) and does not increase with age (i.e. no senescence), $M_x = M_0$;
- 2) Gompertz model. Mortality rate increases exponentially with age as a multiple of the extrinsic mortality rate, $M_x = M_0 e^{\gamma x}$, where γ is the exponential rate of increase in mortality rate with age (Ricklefs & Scheuerlein 2002);
- 3) Weibull model. Mortality rate is comprised of a power function of age added to extrinsic mortality rate, $M_x = M_0 + \alpha x^\beta$, where β characterises the shape of the curve relating mortality rate and age and α determines the magnitude of the mortality rate at any given age for a particular value of β (Ricklefs & Scheuerlein 2002).

There are several proposed measures of the rate of ageing (Promislow 1991; Ricklefs 1998; Ricklefs & Scheuerlein 2001; Williams *et al.* 2006). For this analysis the rate of ageing (ω) measures used have the same units (time^{-1}) for both the Gompertz and Weibull models, and

are equal to $\omega_G = \sqrt{M_0\gamma}$ and $\omega_W = \alpha^{1/(\beta+1)}$, respectively (Ricklefs 1998; Ricklefs & Scheuerlein 2001). Alternative scenarios were simulated under different combinations of M_0 (0.05, 0.2, 0.5, 1.0 yr⁻¹) and ω (0, 0.05, 0.1, 0.15, 0.2 yr⁻¹). The range of M_0 reflected the range of observed instantaneous mortality rate estimates in the data, while the range of ω reflected the range of estimates from most captive and wild mammal populations (Ricklefs 2010b). In each parameter combination, the values were used to solve for γ in the Gompertz model and α in the Weibull model. Given that values for β in the Weibull model are often close to 3 (Ricklefs & Scheuerlein 2001), a value of 3.18 was assumed that represented an estimate from a captive population of red foxes (Ricklefs 2010b). M_x from all models were assumed to vary stochastically (i.e. $M_x = M_x e^\varepsilon$), where ε were obtained from a normal distribution with a mean of zero and a standard deviation of 0.2 (the actual choice of standard deviation value was found to have negligible effect on the bias results).

Mortality rates-at-age were simulated for each ageing model and combination of M_0 and ω . In addition to calculating the mean mortality rate across ages (\bar{M}_x), the numbers-at-age (N_x) were predicted using the simulated M_x values based upon an initial population size at N_0 (age-at-maturity) of 100 animals, $N_{x+1} = N_x e^{-M_x}$. The N_x were assumed to represent a sampled population, allowing the constant mortality rate (\hat{Z}) to be estimated using catch-curve analysis (Ricker 1975). In addition to mortality rate being constant across age classes, catch-curve analysis assumes that aged animals are representative of the age structure in the population and that vulnerability to being sampled is equal at all ages. To perform the analysis, $\ln(N_x)$ was linearly regressed against age class, with \hat{Z} predicted as -1 multiplied by the slope parameter estimated from the regression model. The final step was to calculate the percent relative bias in \hat{Z} , $\text{PRB} = 100(\hat{Z} - \bar{M}_x)/\bar{M}_x$. This procedure was repeated 1,000 times for each ageing model and combination of M_0 and ω . This allowed calculation of the mean PRB under each model scenario given stochastic error in M_x .

These simulation models were modified to examine the bias in Hoenig model Z estimates that might occur as a consequence of using biased data. The predicted N_x were used to obtain the predicted maximum age (\hat{t}_{max}) that would be observed under a given

ageing model and M_0 - ω scenario, defined as the oldest age class that had ≥ 1 animal alive. To generate a sample of Z and t_{\max} data given a rate of ageing (0, 0.05, 0.1, 0.15, 0.2 yr^{-1}), 10 stochastic simulations were performed at each of 20 values of M_0 found within the range 0.05-1 at intervals of 0.05 yr^{-1} . For each ageing model and value of ω , \hat{t}_{\max} , \bar{M}_x , and \hat{Z} were saved from all simulations to yield alternative sets of data containing information on 200 different populations (similar to the observed amount of data) where ageing was or was not assumed to occur. Least squares were then used to estimate the parameters of the Hoenig model (Eq. 5.9) from each of these datasets, given both types of mortality rate data. All data were assumed to belong to one taxonomic group for simplicity. Z for foxes with a maximum age of nine was then predicted using the estimated parameters for each type mortality rate data. Finally, the percent relative bias in Hoenig Z estimates from using constant mortality rate data when senescence was present was calculated as $\text{PRB} = 100 (Z_{\hat{Z}} - Z_{\bar{M}_x}) / Z_{\bar{M}_x}$, where $Z_{\hat{Z}}$ is the predicted Hoenig Z estimate from constant mortality rate data and $Z_{\bar{M}_x}$ is the Hoenig Z estimate obtained from mean mortality rate-at-age data. All analyses were performed using the R statistical software (R Core Team 2013).

5.2.4 Survivorship comparison

Data on the observed age structure of foxes were obtained for different regional populations from across Britain (Kolb & Hewson 1980; Lloyd 1980; Heydon & Reynolds 2000b). These populations were subjected to variable levels of control, of which qualitative information was available to determine the relative levels of control between some regions. The age structure data were used to construct survivorship-at-age (l_x) curves showing the proportion of the first adult age class alive at the start of each later age class x . The juvenile age class (foxes mature in their first winter) was omitted as these data were not usually reported, presumably because the data were usually from culled samples and juveniles were not collected for ageing. Survivorship curves obtained using the two median mortality rate predictions ($l_{x+1} = l_x e^{-M \text{ or } Z}$) were then compared visually to the survivorship curves estimated from the observed age structures.

5.3 Results

5.3.1 McCarthy model

The additional mammal data included on carnivores did not significantly change the estimated scaling exponent for instantaneous mortality rate as a function of body mass, and it remained consistent with the predictions of Savage *et al.* (2004a). The mean of the posterior distribution for the regression coefficient b was -0.269 . The 95% credible interval was $[-0.348, -0.189]$, encompassing both the predicted value of -0.25 and the alternatively hypothesised value of -0.33 .

Of the random effects included in the model, taxonomic order (θ) exhibited the greatest level of variation, with the median of the posterior for the standard deviation (v) equal to 1.158 (Figure 5.6). There was comparatively little variation among species, with the median of the posterior distribution for the standard deviation (φ) of the random effect for species (ζ) equal to 0.152. The posterior distributions of each of the random effects were also examined to determine their relative importance to the model. All apart from the random effects for species differed significantly from zero, i.e. the distributions all overlapped zero (Figure 5.7), suggesting that this random effect could be dropped. For the model including the random effect for species the DIC was -392.6 , compared to the DIC for the model excluding this random effect of -393.9 . The lower value shows slight support for the model where the random effect for species was dropped.

The actual choice of model had minimal impact on the predicted M for British foxes as the difference between models incorporating the random effect for species was negligible, with the posterior mean and median of M being almost identical and the width of the 95% credible intervals differing by only 0.01 between the two models. From the model with the random effect for species dropped, the predicted M posterior mean was 0.319, the posterior median was 0.274 and the 95% credible interval was $[0.095, 0.793]$. The coefficient of variation (CV) was 0.600, indicating the low precision of the predicted distribution.

The effect of including the additional data for Carnivora resulted in the predicted M for a given body mass being both slightly higher and more precise compared to the original dataset (Figure 5.8). This difference became greater at smaller body masses where there were fewer survival estimates contained in the original dataset. For foxes the difference in predicted M was not large – the posterior median from the original dataset analysis was 0.225 compared to 0.274 – but the CV from the original dataset analysis was higher with a value of 0.703 compared to 0.600.

Sensitivity analysis of the predicted M to dropping a taxonomic order from the data revealed that orders Artiodactyla and Carnivora had most influence; this was not unexpected as these orders also had the greatest number of mortality rate estimates (Figure 5.1) so would carry more weight in the analysis (Figure 5.9a). Removal of the Artiodactyla data resulted in the posterior median increasing to 0.366 from 0.274, while removal of the Carnivora data resulted in a slight decrease to 0.262. (N.B. not including the Carnivora data resulted in an invalid prediction of M for foxes as the order random effect could not be included).

Several statistical distributions were fitted to the predicted posterior for M to determine the appropriate distribution for use as a prior. Of those selected, the lognormal distribution gave the best fit as shown by the Kolmogorov-Smirnov GOF test p -value equal to >0.99 . None of the other distributions (gamma, generalised gamma) gave p -values >0.05 so these were not considered further. The McCarthy prior for M was therefore assumed to be lognormally distributed.

5.3.2 Hoenig model

There were significant differences in the estimation error of the mortality rate estimates between the taxonomic groups, as shown by the posterior distributions for standard deviation of the $\ln(Z)$ deviates (Figure 5.10). A model with pooled estimation error across groups was therefore unsuitable as the degree of uncertainty in the Z estimate would be underestimated. The non-pooled model was supported by DIC, as the model with pooled estimation error had a value of -181.2 compared to -202.0 for the model with non-pooled estimation error.

A comparison of the non-hierarchical and hierarchical model structures revealed minimal differences in predicted mortality rate, as shown by the prediction of carnivore mortality rate as a function of maximum age (Figure 5.11). The difference in DIC between models was too small to reliably choose between them, with a difference of <2 in weak support of the hierarchical model. Although there were no differences in predicted mortality rates, there were large differences in the slope and intercept parameter estimates between the two model structures (Figure 5.12). The slope parameter estimates for all groups showed shrinkage towards the hierarchical posterior predictive distribution (posterior mean of -0.97), for carnivores the non-hierarchical estimate was -1.38 compared to the hierarchical estimate of -1.11 . Given the large variation in the carnivore mortality rate data, particularly at older maximum ages, this was expected. The shrinkage was not as marked for the intercept parameter estimates for each group because the posterior predictive distribution (posterior mean of 1.30) was highly uncertain. For carnivores, the difference in estimates between the two models was instead dictated by the correlation between the slope and intercept, as the non-hierarchical posterior mean of 2.03 compared to the hierarchical posterior mean of 1.29 , which was lower than the predictive posterior mean due to the change in slope.

The predicted Z for a British fox of maximum age nine years was similar between models, with the posterior and median of predicted Z being almost identical and the width of the 95% credible intervals differing by only 0.01 . From the hierarchical model, the predicted Z posterior mean was 0.543 , the posterior median was 0.469 and the 95% credible interval was $[0.163, 1.371]$. The CV was 0.594 , indicating a similarly low level of precision of the predicted distribution when compared to the McCarthy model estimate.

Sensitivity analysis of the predicted Z to dropping a taxonomic group from the data revealed that the fish group had most influence, this was not unexpected as this group had the greatest range and number of mortality rate estimates (Figure 5.4) so would carry more weight in the analysis (Figure 5.9b). Removal of the fish group data resulted in the posterior median increasing to 0.552 from 0.466 , and caused the CV to increase to 0.366 from 0.594 .

Examination of the bias that would result from incorrectly assuming the maximum age of British foxes was nine found that if the true maximum age was higher, Z was

overestimated, with the PRB equal to 12%, 24% and 35% if the true maximum age was 10, 11, or 12 years respectively. Conversely, Z was underestimated if the true maximum age was less than nine, with the PRB equal to -9%, -21% and -33% if the true maximum age was 8, 7, or 6 years respectively.

5.3.3 Bias due to the constant mortality-at-age assumption

The bias in age-constant \hat{Z} estimated using catch-curve analysis compared to mortality rate estimated as the mean across all ages (\bar{M}_x) from alternative ageing model scenarios was small (mean PRB of 0-10%) when extrinsic mortality rate was relatively high and the rate of ageing was low (Table 5.1). As expected, constant \hat{Z} were underestimated more as extrinsic mortality rate decreased and the rate of ageing increased, resulting in larger negative bias. The largest mean PRB (-53.8%); from the Gompertz model with M_0 of 0.05 yr^{-1} and ω of 0.2 yr^{-1} , resulted from the constant \hat{Z} estimate being 0.477 yr^{-1} compared to 1.054 yr^{-1} for \bar{M}_x (both calculated as the means of simulated values).

The Hoenig Z estimates were also negatively biased (Table 5.2). As expected, the PRB increased as the rate of ageing increased. In all scenarios, the difference in Z estimates was $<0.1 \text{ yr}^{-1}$ except for the scenario with largest PRB (-25.2%) where ageing was assumed to occur according to the Weibull model and ω was 0.2 yr^{-1} . Under this scenario, the difference was 0.137 yr^{-1} (estimated Z was 0.405 yr^{-1} compared to 0.542 yr^{-1}).

5.3.4 Mortality rate prior

The posterior predictions for fox mortality rate from the McCarthy and Hoenig models that could be used to establish a prior probability distribution were both lognormal (Figure 5.13). Though not significant, the parameters of the distributions differed, with the mean of $\ln(M)$ equal to -1.300 (i.e. median M of 0.274) from the McCarthy model and mean of $\ln(Z)$ equal to -0.76 (i.e. median Z of 0.469) from the Hoenig model. As expected, the total mortality rate estimate Z from the Hoenig model was higher than the natural mortality estimate from the McCarthy model.

The predicted survivorship curves using the McCarthy M and Hoenig Z estimates (Figure 5.14) show that the curve using the Hoenig Z was the closest to the observed range of survivorship curves, with the closest curve (W Wales) relating to a population noted to have been under minimal culling pressure and the furthest away from one (Isle of Skye) noted to have been under heavy culling pressure (Lloyd 1980).

5.4 Discussion

5.4.1 Credibility of alternative priors

Bayesian informative prior probability distributions were established from the predictive posteriors for the instantaneous non-culling mortality rate of British foxes using two alternative meta-analytic life history methods. The total mortality rate estimate Z from the Hoenig model based upon maximum age and assumed to equal natural mortality rate in populations experiencing minimal anthropogenic mortality factors was higher than the estimate for M from the McCarthy model based upon body mass. This was to be expected as Z cannot be less than M , but the difference between the two predictions was larger than expected. Due to the uncertainty in both priors, shown by high CV, the 95% credible intervals overlapped considerably but the median estimates differed by almost 0.2 yr^{-1} . Sensitivity analyses showed that despite there being an effect of removing certain taxonomic groups, the difference between median estimates from the two models was still greater than 0.1 yr^{-1} . Given this difference, choosing one prior over the other could greatly affect inference from population dynamics models and influence management decisions (Clark 1999). It is therefore useful to determine which prior is the most credible choice.

Data on rural British fox mortality are limited for direct comparison, this reason being the motivation for applying the meta-analytic methods. An estimate from Japan for annual natural mortality rate was 0.34, i.e. M was 0.416 yr^{-1} (Uraguchi *et al.* 2014) appears to support the Hoenig model estimate, with the slightly lower value due to higher maximum age of foxes in Japan (Maekawa, Yoneda & Togashi 1980). The only mortality estimate for a rural population in Britain (Dorset) comes from a very small sample ($n=8$) that found annual non-culling mortality rate was 0.14, i.e. M was 0.15 yr^{-1} (Reynolds & Tapper 1995a). This

value is only just encompassed by the 95% credible intervals for both models. In contrast, data from a well-studied urban population (Bristol) suggest that natural mortality is much higher, as annual adult natural mortality rate was 0.505 for males and 0.468 for females (Harris & Smith 1987), i.e. M was 0.703 yr^{-1} and 0.631 yr^{-1} respectively. Rural and urban sources of natural mortality on foxes are likely to be quite different, but the conflicting natures of rural and urban estimates do not appear to lend much credibility for either prior in each situation.

The relative credibility of each prior was further explored by comparing survivorship curves constructed using available data on age structure of different regional rural fox populations with predicted survivorship curves constructed using the median posterior predictive mortality rate estimates from both models. The regional fox populations were subjected to variable levels of deliberate culling and so do not represent natural survivorship, but nevertheless are useful for comparison. The Hoenig survivorship curve was most similar to populations that were known to have suffered only minimal culling mortality, e.g. west Wales (Figure 5.14), while curves that differed most were from heavily culled populations where Z was very high, e.g. Isle of Skye (Lloyd 1980). The McCarthy survivorship curve was not similar to any of the regional survivorships, and also implies that the maximum age observable in a fox population with this M is >15 years. This age is unprecedented in wild European fox populations (Mulder 2004); 14 years is the maximum age reported (Maekawa, Yoneda & Togashi 1980), but from Japan where foxes are heavier than in Britain (Macdonald & Reynolds 2004) which would alter both mortality estimates. Captive foxes have however been documented to survive to >14 years and older (Carey & Judge 2000; Baker & Harris 2008). The survivorship data therefore suggest that the McCarthy model estimate is an underestimate of the M experienced by wild populations.

One explanation of the difference between the Hoenig and McCarthy model estimates is the natural mortality factors described by each. Predictions based upon maximum age in observed samples using the Hoenig model include both intrinsic and extrinsic mortality factors as both will limit maximum age. In contrast, the predictions based upon metabolic theory using body mass data using the McCarthy model are influenced only by intrinsic

mortality factors. The difference between the estimates therefore depends upon the relative importance of intrinsic and extrinsic mortality factors and their relationship. Field data from a wide range of taxonomic groups suggest that much of the heterogeneity in mortality rate can be predicted by allometric relationships that reflect only intrinsic mortality, despite the many extrinsic mortality factors that are found in nature (McCoy & Gillooly 2008), perhaps because many ecological factors that lead to extrinsic mortality risk (competition, predation) may be ultimately also constrained by individual metabolic rate (Peters 1983; Brown *et al.* 2004). There is, however, considerable variability in mortality rate estimates scaled by body mass between taxonomic orders, as captured by the order random effect. This means extrinsic factors may be relatively more important than predicted for species from certain orders. Predictions from the McCarthy model may therefore underestimate mortality rate for some species as the additional extrinsic mortality risk is not accounted for by the allometric relationship.

This explanation assumes that the relationship between intrinsic and extrinsic mortality risks is additive, and that most ageing-related death is caused by intrinsic factors, such as tumours or cardiovascular failure, rather than increased vulnerability to extrinsic factors (Ricklefs 2008, 2010a). However, it is probable that there is an interaction between the risks making it difficult to separate them (Nussey *et al.* 2008). For example, the cumulative effects of cell damage with age may increase mortality from extrinsic factors by increasing vulnerability to predation (Wright *et al.* 2006) or by reducing ability of predators to hunt (MacNulty *et al.* 2009). Likewise, catastrophic declines in condition just prior to death may reflect terminal disease rather than senescence (Coulson & Fairweather 2001), although the likelihood of contracting such an illness may increase with age (Nussey *et al.* 2008).

The mortality risk interactions are further complicated in the presence of density-dependence causing compensatory effects between mortality factors, with extrinsic mortality risk expected to be greater in high-density populations. Taking foxes as an example, the extrinsic mortality from predation and competition is generally low and is not a major factor (Macdonald & Reynolds 2004). However, the risk from other factors can be high, e.g. from

sarcoptic mange (Soulsbury *et al.* 2007) but it appears to be density-dependent (Lindström 1992). Given that the mortality rate data upon which these meta-analyses are based reflect both types of mortality risk, this makes it difficult to simply interpret the difference between the Hoenig and McCarthy model estimates as extrinsic mortality. That captive fox populations, assumed to be under very low extrinsic mortality risk and receiving veterinary care, can survive to the maximum ages predicted by the McCarthy model estimate suggests that extrinsic mortality could however account for a large amount of the difference.

5.4.2 Other anthropogenic mortality factors

These conclusions are also affected by the validity of some of the assumptions either made by each model or made about the data. One assumption was that the mortality rate data were from populations that suffered only minimal anthropogenic disturbances. Incorporated studies were screened to remove those that noted obvious effects, especially in relation to culling or harvesting, but it is likely that many of the mortality rate data included some level of anthropogenic mortality because few populations exist in pristine, untouched habitats. Two problems arise from this. Firstly, the mortality rates used to fit the models would be higher than M from untouched populations, so the results from both models would be overestimates. Secondly, if there was a compensatory relationship between natural and anthropogenic mortality factors, the natural mortality rate in a population would be lower than without any anthropogenic mortality, also leading to overestimation. It is also possible that body masses and maximum ages would be lower due to the additional anthropogenic mortality, also resulting in mortality rate being overestimated.

One anthropogenic mortality factor potentially present in the terrestrial mammal data (i.e. not Sirenia, Cetacea, Otariidae and Phocidae) that is not accounted for is from RTC. Roads and railroads are a widespread feature on most landscapes and few terrestrial species are immune to being killed on roads (Trombulak & Frissell 2000). Across species RTC are generally nonspecific with respect to adult age, sex, and body condition when considered annually (e.g. Davies, Roper & Shepherdson 1987; Bangs, Bailey & Portner 1989; Baker *et al.* 2007; Grilo, Bissonette & Santos-Reis 2009), although there may be seasonal differences

for juveniles. For example, there may be more casualties of juvenile male foxes during the dispersal period (Baker *et al.* 2007), but the annual mortality of dispersing and non-dispersing foxes is similar (Soulsbury *et al.* 2008). It might therefore be assumed that RTC is a component of the entire mortality rate dataset, meaning that M would be overestimated by a constant amount using either model. However, this is complicated by the suggestion that larger mammals are killed less often than expected (Ford & Fahrig 2007; Barthelmess & Brooks 2010) and that the effect of RTC is likely to be dependent upon both the species and study location, i.e. some species are more at risk to crossing roads than others, and some locations have higher road densities. An effect of study location latitude on mortality rate was excluded from the McCarthy model previously, suggesting location was not a key variable (McCarthy, Citroen & McCall 2008). Knowledge of the road density in each study location would be required to further understand the effect of location on RTC mortality; as these data were not available it was not examined. There are considerable negative impacts on local abundance for populations of species that suffer high incidence of road mortality (Trombulak & Frissell 2000; van Langevelde & Jaarsma 2004; Fahrig & Rytwinski 2009; van Langevelde, van Dooremalen & Jaarsma 2009); however, there appears to be a variable effect between different taxa, e.g. RTC contribute to only a minor part of the annual mortality for many ungulate populations (Groot Bruinderink & Hazebroek 1996). This makes it impossible to correct the data for RTC mortality, leading to the assumption that it must be minimal to be able to make inferences about M .

The Hoenig model is more robust to estimation in the presence of RTC mortality data contamination as it estimates Z , rather than M . An additional point to consider is that the parameter of interest in population dynamics modelling is not in fact natural mortality, but non-culling or non-harvest mortality. If there is a considerable component of RTC mortality then M will be underestimated by the McCarthy model as strictly it estimates natural mortality, not non-culling mortality. Mortality from RTC might indeed explain the difference between the McCarthy and Hoenig model estimates. The implied annual mortality rate difference between the McCarthy and Hoenig models was 13%. A Swedish study used driver questionnaires to estimate the number of animals accidentally hit and used a national population estimate for foxes to estimate an annual RTC mortality rate of 9%

(Seiler, Helldin & Seiler 2004). Although a small component of total mortality in this Swedish population, this would account for much of the difference between instantaneous non-culling mortality estimates in this study. Given that it is non-specific, the Hoenig model can view RTC mortality as an additional extrinsic mortality factor and give a less biased estimate of Z .

There is also argument that for a rural fox mortality rate prediction, RTC mortality is perhaps not a major issue. In urban populations where road traffic density is high, there can be a large impact from roads on fox mortality, particularly when crossing major roads (Harris & Smith 1987; Baker *et al.* 2007); but in rural areas the regional variations in fox density are better explained by differences in culling effort rather than road traffic density (Heydon & Reynolds 2000b). In general, based upon their relative frequencies carnivores are less likely to be killed on roads compared to herbivores and omnivores (Ford & Fahrig 2007; Barthelmess & Brooks 2010; Cook & Blumstein 2013). This implies that there is behavioural avoidance of roads by carnivores, particularly those roads with high traffic volume (Grilo, Bissonette & Santos-Reis 2009). In accordance, urban foxes have been shown to cross roads less than expected based upon random movement and also to cross more after midnight when traffic density is less (Baker *et al.* 2007).

5.4.3 Reliability of data

Different methods were used to obtain the mortality rate data, potentially leading to considerable differences in their precision. The cetacean, fish and mollusc data were estimated using catch-curve analysis (Ricker 1975; Deriso, Quinn & Neal 1985), while the carnivore and other mammalian data used either mark-recapture models (Lebreton *et al.* 1992; White & Burnham 1999) or Kaplan-Meier survival analysis (Kaplan & Meier 1958; Pollock *et al.* 1989). Sample sizes used to estimate mortality rate for mammals were relatively small compared to the others, which further confounded the precision. The McCarthy model explicitly incorporated the estimate standard error, while the Hoenig model did not. The modelling of different standard deviation in $\ln(Z)$ deviates for each taxonomic group did however effectively account for the differences in precision due to estimation

method because the methods used were constrained to particular taxonomic groups. Nevertheless, there was considerable variation in precision within taxonomic groups that was not incorporated. For example, the black bear Z estimates were considerably higher than the Z estimates for other Ursidae species (Figure 5.5), but also had a much larger standard error. These estimates affected inference from the Ursidae data. It would be preferable to incorporate such differences in estimate precision explicitly into the Hoenig model, but this would require new Z estimates with standard errors from minimally impacted populations for the non-carnivore groups, which are not available.

The size of the sample from which t_{\max} was estimated was also not considered in the Hoenig model. As they are rare, old animals are more likely to be found only in large samples. This means smaller samples will underestimate t_{\max} , causing the model to underestimate Z . This is less of a problem in samples for species in which Z increases sharply with age, but more so in long-lived species where it becomes dependent upon the accuracy of the age-determination technique and the sample size (Beverton & Holt 1959). Hoenig (1983) showed that t_{\max} tends to increase slower with increasing sample size once a sample of 200 animals has been examined. The abundance of carnivore populations is generally quite low and determining age is invasive (e.g. by tooth sectioning); consequently the majority of field studies have only differentiated between juveniles and adults, meaning that studies with aged samples are themselves rare. This makes the sample size problem greater for carnivores, as samples that are aged are relatively small compared to the other taxonomic groups. Few studies will have sample sizes of >200 animals, particularly in populations that are not harvested or controlled. For culled species such as foxes, aged samples are usually large enough, but these culled populations do not satisfy the assumption of minimal anthropogenic impact. This means it is possible that t_{\max} data for carnivores are all underestimates, causing a further exaggeration of the difference between the Hoenig and McCarthy model estimates. If the maximum age used to predict Z for foxes was an underestimate, then in theory if the 'true' maximum age was used the Hoenig model estimate would become more similar to the McCarthy model estimate. However, such a low estimate is not supported by the survivorship curve comparisons.

5.4.4 Effect of senescence

Despite widely held views that senescence could not occur in wild populations because animals would not survive to old age in such adverse conditions, it is now well-documented in wild terrestrial vertebrates (see Jones *et al.* 2008). This causes the pattern of Z across ages to show a U-shape, where the mortality is higher in juvenile and older adult age classes. Few studies in the mammalian dataset attempted to determine whether senescence was occurring by estimating age-specific Z , and instead reported only a single Z assumed to be constant across all adult ages. This assumption was also made about Z estimated using catch curves. The bias analysis due to the constant mortality rate-at-age assumption showed that estimates of Z from catch-curve analysis are underestimates of the actual mean mortality rate, and the negative bias becomes worse as ω increases and as M_0 decreases, under the explanation that more individuals will survive long enough to reach the age classes where senescence occurs. It is likely that most datasets actually contain species covering a range of values for ω , meaning the results at $\omega = 0.2 \text{ yr}^{-1}$ represent a worst case scenario about the degree of negative bias that would be found.

The Gompertz and Weibull models both assume that senescence begins at the age-at-maturity, and both have empirical support in mammalian species (Ricklefs & Scheuerlein 2002; Gaillard *et al.* 2004). However, there is some evidence that the age at onset of senescence is often later than the age at maturity (Promislow 1991). An alternative 3-phase model attempts to account for this by determining an age of senescence and having 3 constant Z phases (Sibly *et al.* 1997). This model was not examined here as a constant Z for all older age classes is unlikely; but if senescence were to begin later then bias from assuming constant adult Z would be further reduced. The Gompertz and Weibull models also both assume that intrinsic and extrinsic mortality factors can be distinguished. As discussed above this is not always possible if there is an interaction between them; but for the purpose of evaluating bias in the data it seems reasonable here.

The negative bias in the data could affect the Hoenig model estimates directly, but the model itself also makes an assumption of constant Z , so given the Hoenig model prior for

foxes appears to be the more credible prior established by the two methods, the effect of this assumption is important to understand. By assuming constant Z across ages, the Hoenig model makes an implicit assumption that any senescence occurs after t_{\max} , i.e., negligible senescence. For foxes, there is contrasting evidence for senescence. Lloyd (1980) indicated that Z did not vary with age in a population from Wales, and this lack of survival senescence is supported by the estimated young and old adult Z from the USA both being 0.6 yr^{-1} (Sibly *et al.* 1997). In these cases, ω is zero and the Hoenig model estimate is not biased.

However, reproductive senescence (i.e. increased proportion of non-breeding animals and reduced litter sizes) has been shown to occur in urban fox populations during the fifth and sixth breeding seasons (Harris 1979), and a study on a captive population of foxes found ω to equal 0.102 yr^{-1} (Ricklefs 2010b). Given that ω in wild and captive populations are similar (Ricklefs 2010a), this suggests that the Hoenig model would be an underestimate with a PRB of -5% . This does not represent a major difference in the median value for the Hoenig model prior for Z , and given the relatively large CV it is unlikely to have any effect on the inference from population dynamics models. Where reliable data exist on ω in the wild for a given species, it should therefore be possible to produce a senescence correction factor for Hoenig model estimates.

5.4.5 Summary

In conclusion, based upon regional survivorship curves and maximum ages it seems that the Hoenig model prior is more credible when compared to the McCarthy model prior, although there are reasons to believe that it may be slightly biased in either direction. For pedantic reasons, it is of interest to apply both priors and determine the effects of a supposedly correct versus incorrect prior on inference from population dynamics models. Moreover, for the preferred prior it would be important to perform further sensitivity analyses to evaluate the effects of plausible alternative formulations of the prior on possible management decisions. This could help to indicate the potential value of implementing field studies to obtain more precise estimate of the non-culling mortality rate of red foxes.

5.5 Tables

Table 5.1. Mean percent relative bias (PRB) from 1,000 simulations where mortality rate estimated using catch curve analysis (\hat{Z}) was compared to the mean mortality rate across ages (\bar{M}_x) from a predicted population using alternative combinations of extrinsic mortality rate and rate of ageing under different models of ageing. For each simulation, the stochastic error in M_x was assumed to follow a normal distribution with a mean of zero and a standard deviation of 0.2 yr^{-1} .

Model	Rate of ageing, ω (yr^{-1})	Extrinsic mortality rate, M_0 (yr^{-1})			
		0.05	0.2	0.5	1.0
Constant	0	-0.1	-0.3	-0.3	-0.6
Gompertz	0	-0.1	-0.3	-0.3	-0.6
	0.05	-7.3	-0.8	-0.6	-0.9
	0.1	-22.3	-3.8	-1.5	-1.2
	0.15	-37.5	-8.8	-3.0	-2.0
	0.2	-53.8	-15.5	-4.7	-3.0
Weibull	0	-0.1	-0.3	-0.3	-0.6
	0.05	-16.8	-2.2	-0.4	-0.8
	0.1	-25.7	-11.5	-1.7	-0.8
	0.15	-31.7	-20.0	-5.7	-1.3
	0.2	-36.5	-26.8	-11.2	-2.6

Table 5.2. Percent relative bias of Hoenig model Z predictions for foxes (maximum age of nine) made using estimates of constant mortality rate from catch curve analysis (\hat{Z}) compared to using estimates of mean mortality rate across ages (\bar{M}_x) from data simulated using different ageing models and assumed rate of ageing.

Rate of ageing, ω (yr ⁻¹)	Constant	Gompertz	Weibull
0	-0.3	-0.3	-0.3
0.05	---	-1.0	-1.9
0.1	---	-4.2	-6.3
0.15	---	-9.3	-14.6
0.2	---	-18.5	-25.2

5.6 Figures

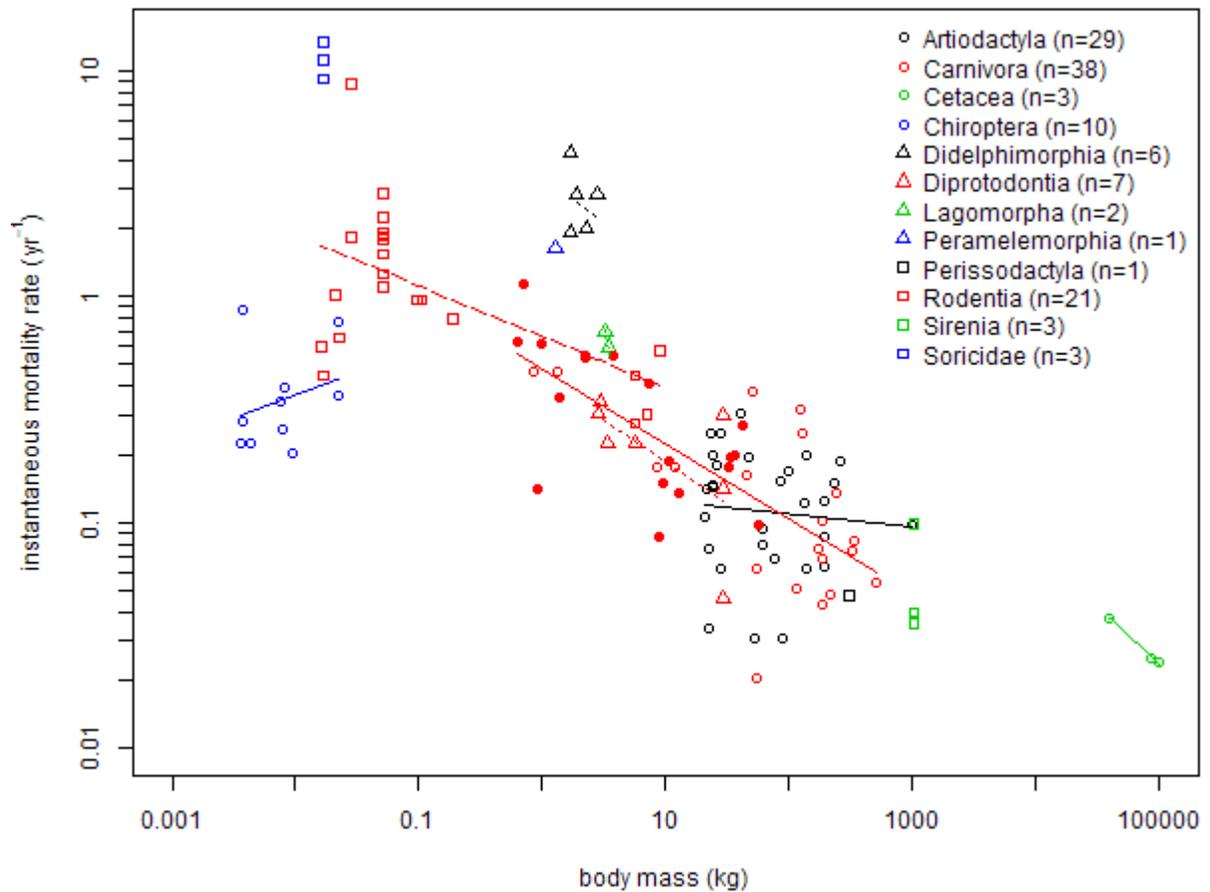


Figure 5.1. Mammalian instantaneous mortality rate data (transformed from mean annual survival rate estimates) for 12 orders plotted against body mass. The number of estimates within each order is indicated in parentheses. Filled symbols relate to Carnivora data added to the McCarthy *et al.* (2008) dataset. Also shown are linear models (fit by least squares) through the range of data for each order (solid lines relate to data shown by circle symbols, dotted lines relate to triangles and dashed lines relate to squares).

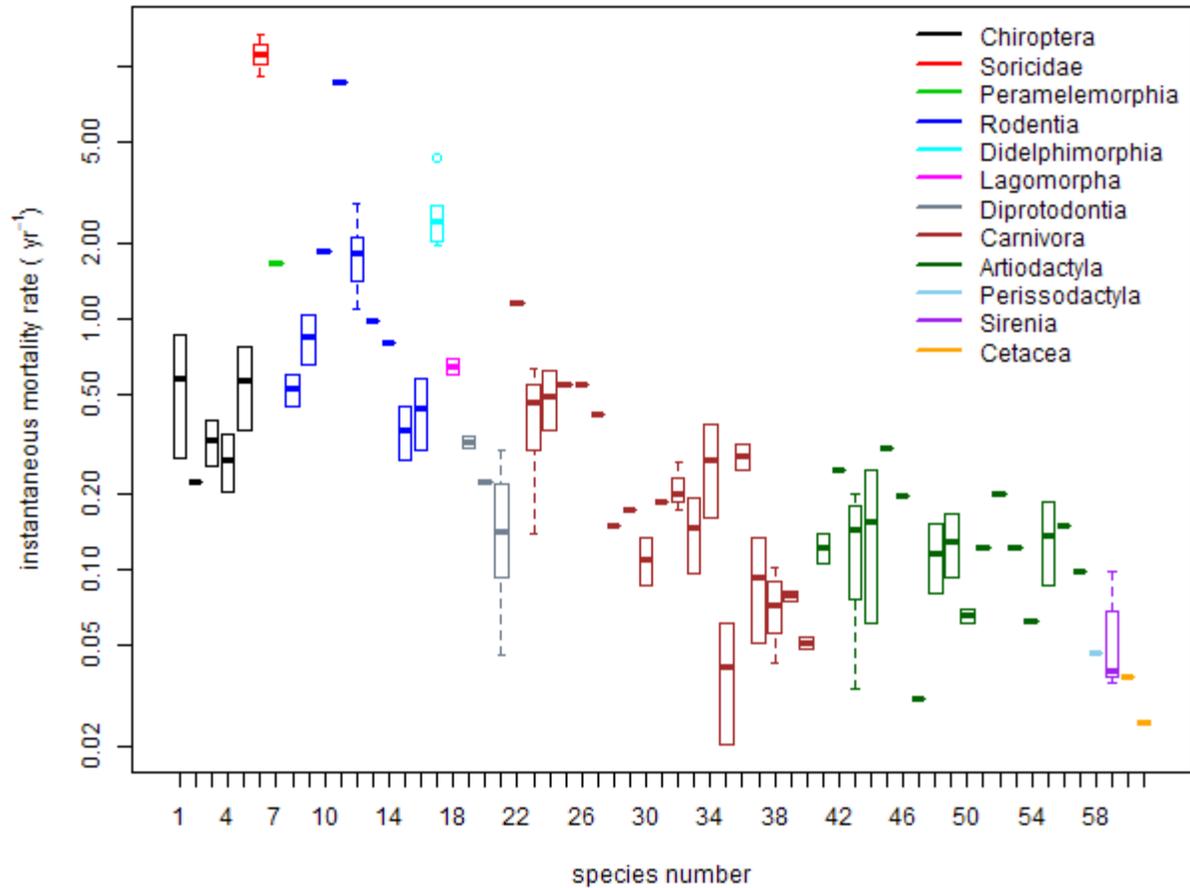


Figure 5.2. Instantaneous mortality rate data (transformed from mean annual survival rate estimates) for each species. Species are grouped by taxonomic order, which are ranked by increasing body mass (L-R). For species which had more than one estimate (i.e. from different sexes or studies), box plots indicate the variability in these mean estimates.

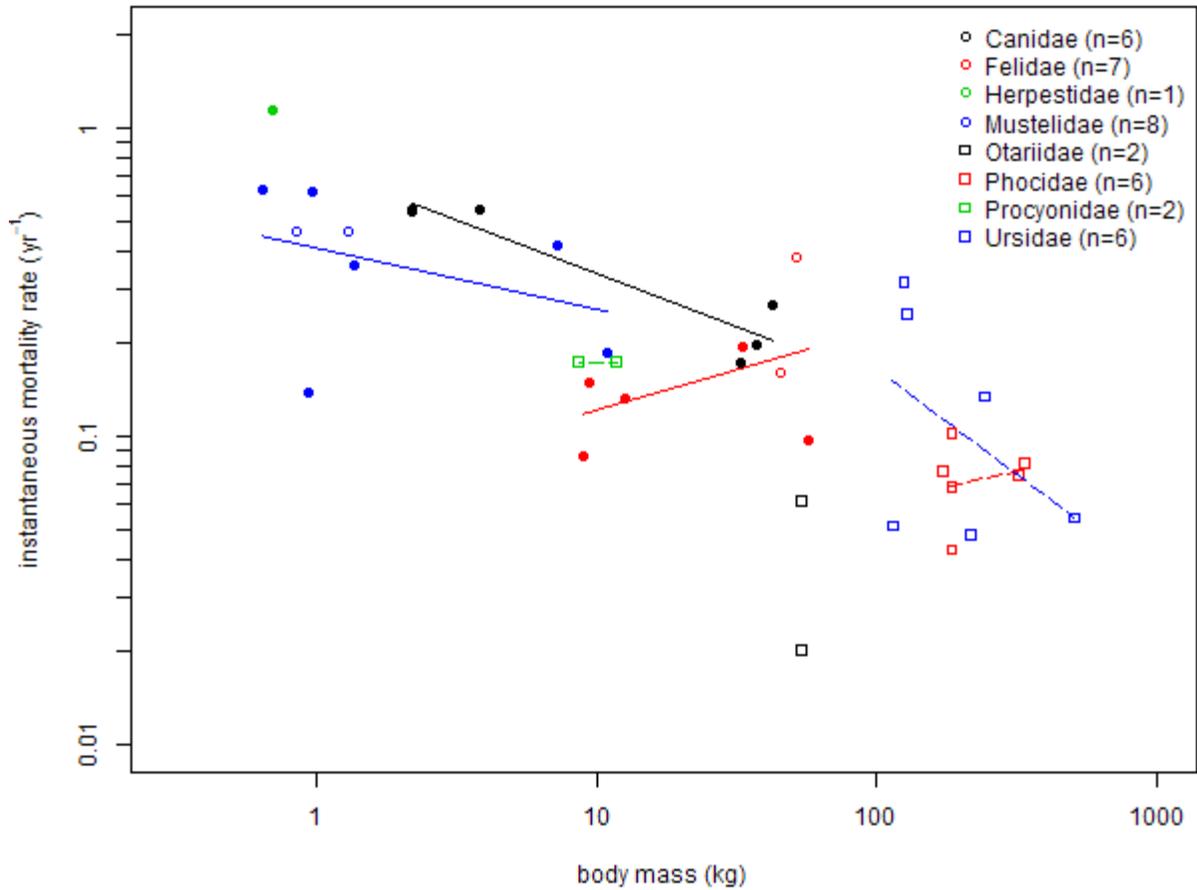


Figure 5.3. Carnivore instantaneous mortality rate data (transformed from mean annual survival rate estimates) for 8 families plotted against body mass. The number of estimates within each family is indicated in parentheses. Filled symbols relate to data added to the McCarthy *et al.* (2008) dataset, including all Canidae. Also shown are linear models (fit by least squares) through the range of data for each family (solid lines relate to data shown by circle symbols and dashed lines relate to squares).

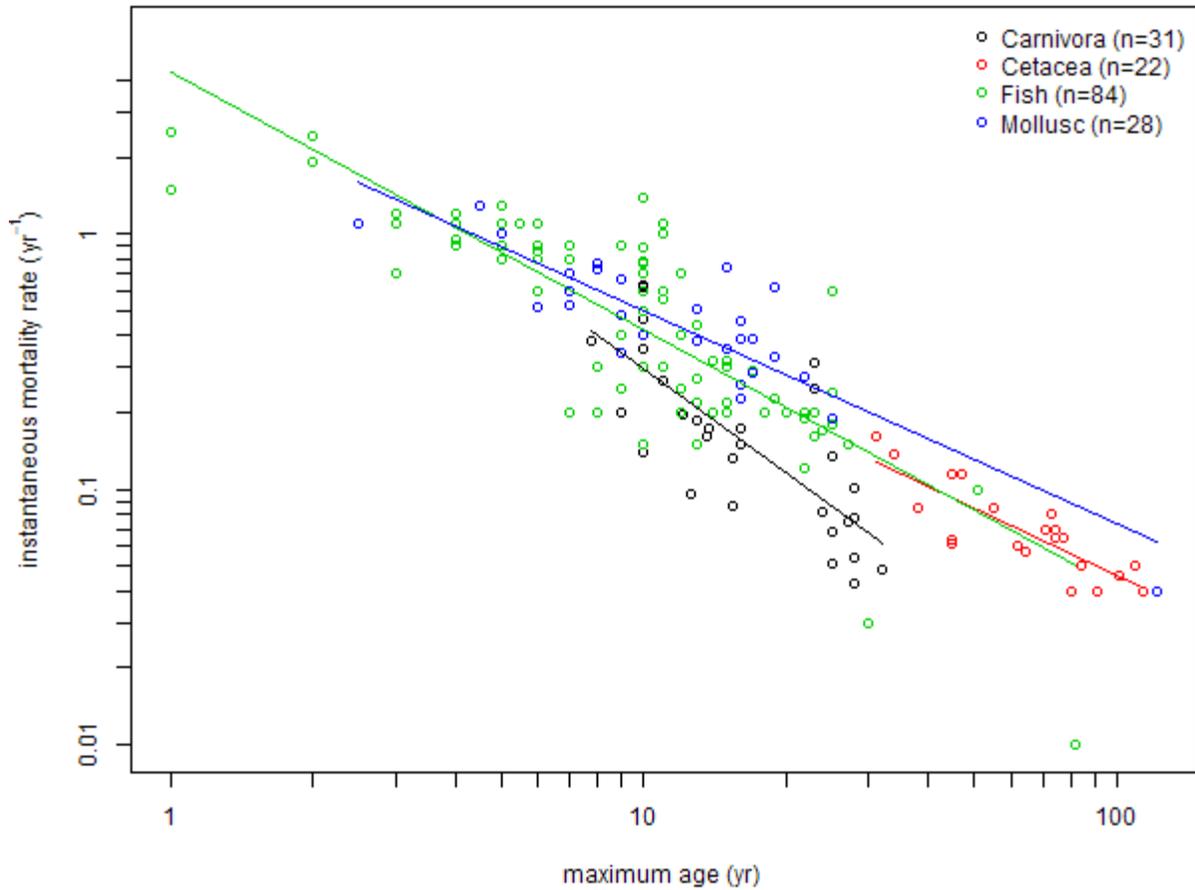


Figure 5.4. Instantaneous mortality rate data for each of the taxonomic groups included in the Hoenig model plotted against the maximum age recorded for that species population (or the most geographically local population for which data existed – see 5.2.2). The number of estimates within each group is indicated in parentheses. Also shown are linear models (fit by least squares) through the range of data for each group.

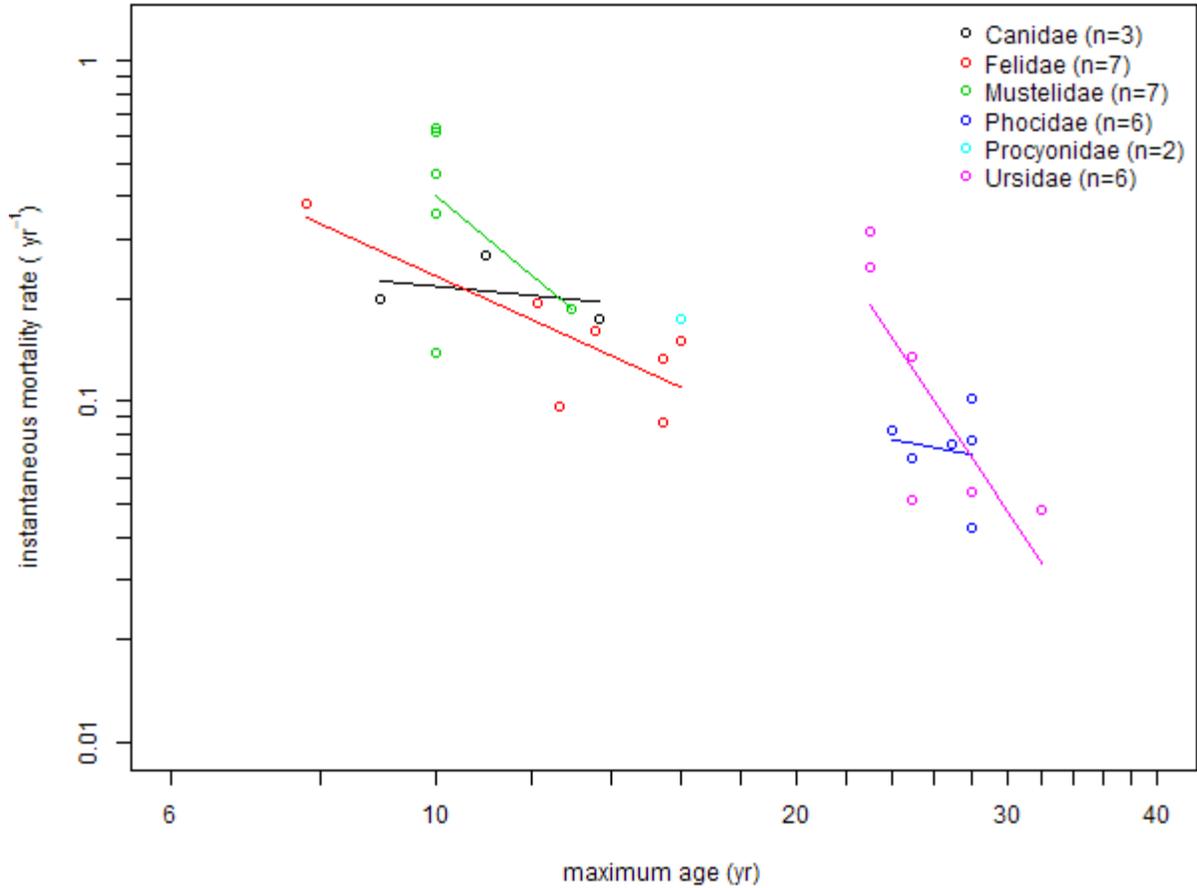


Figure 5.5. Carnivore instantaneous mortality rate data for 6 families included in the Hoenig model plotted against the maximum age recorded for that species population (or the most geographically local population for which data existed – see 5.2.2). The number of estimates within each family is indicated in parentheses. Also shown are linear models (fit by least squares) through the range of data for each family.

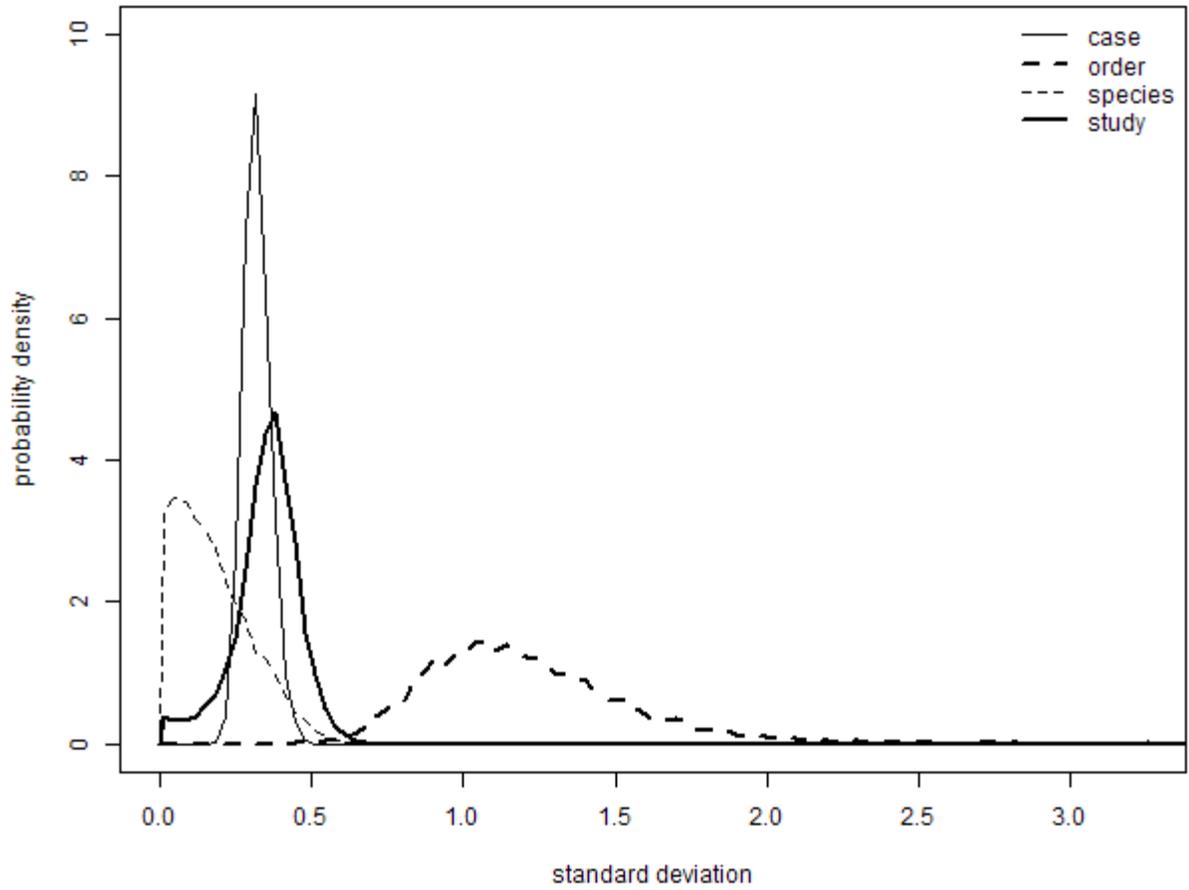


Figure 5.6. Posterior probability distributions of the standard deviation in each of the random effects included in the McCarthy model to show the relative variation attributable to each effect.

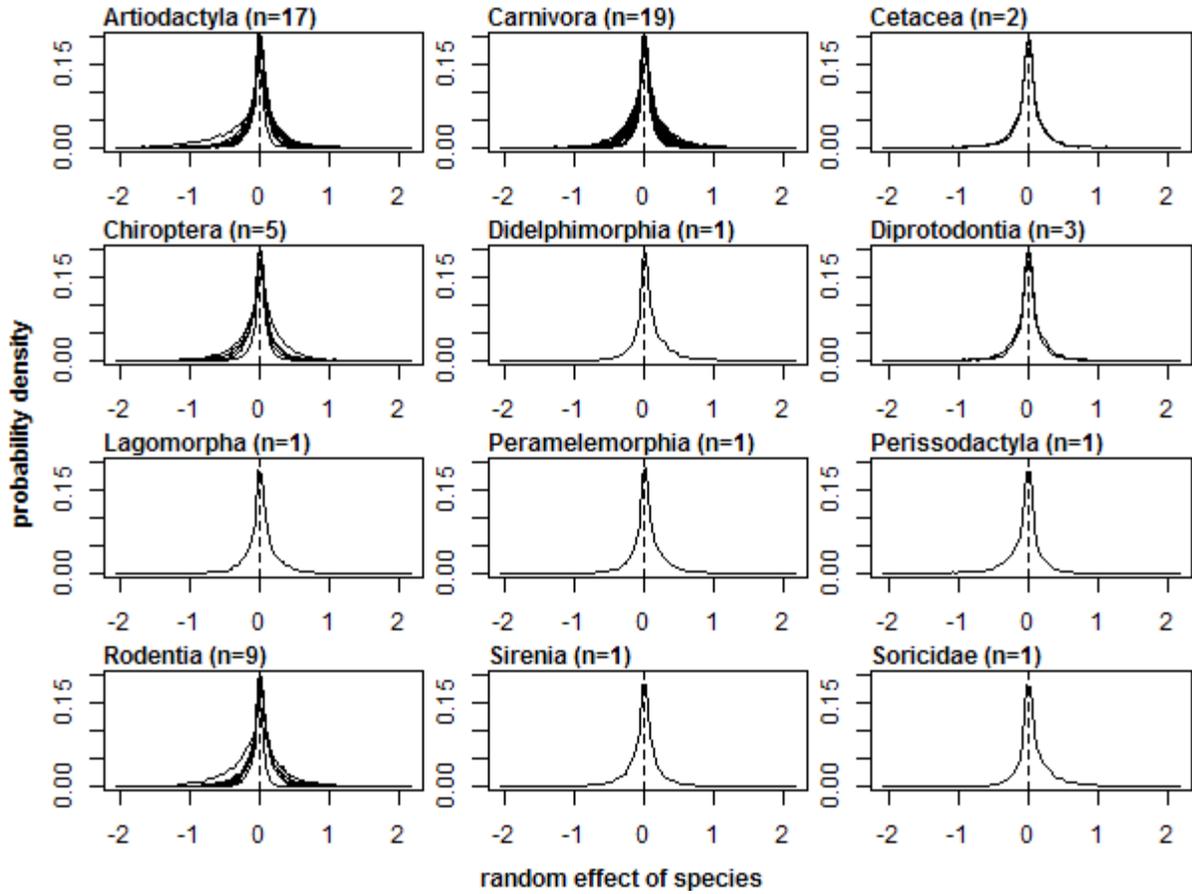


Figure 5.7. Posterior probability distributions for the random effects of each species included in the McCarthy model. Species random effects are shown grouped by taxonomic order. The number of species in each order is indicated in parentheses. Dashed vertical lines indicate zero effect.

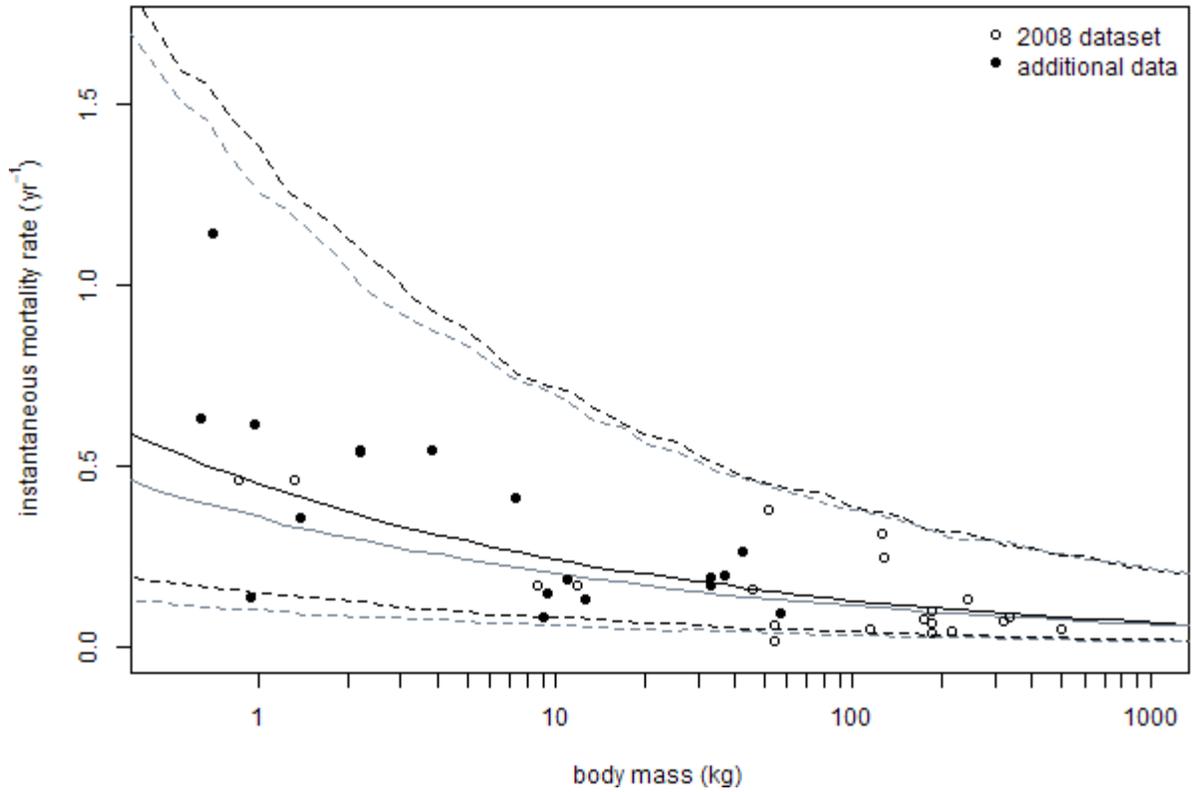


Figure 5.8. Predicted allometric relationship between instantaneous adult mortality rate and body mass for species from the Carnivora order. Predictions are shown from an analysis using the McCarthy *et al.* (2008) dataset (grey lines) and from an analysis including the additional data (black lines). Solid lines show the posterior median prediction and the dashed lines the 95% credible interval. Each mean mortality rate estimate from the database is shown by a circle.

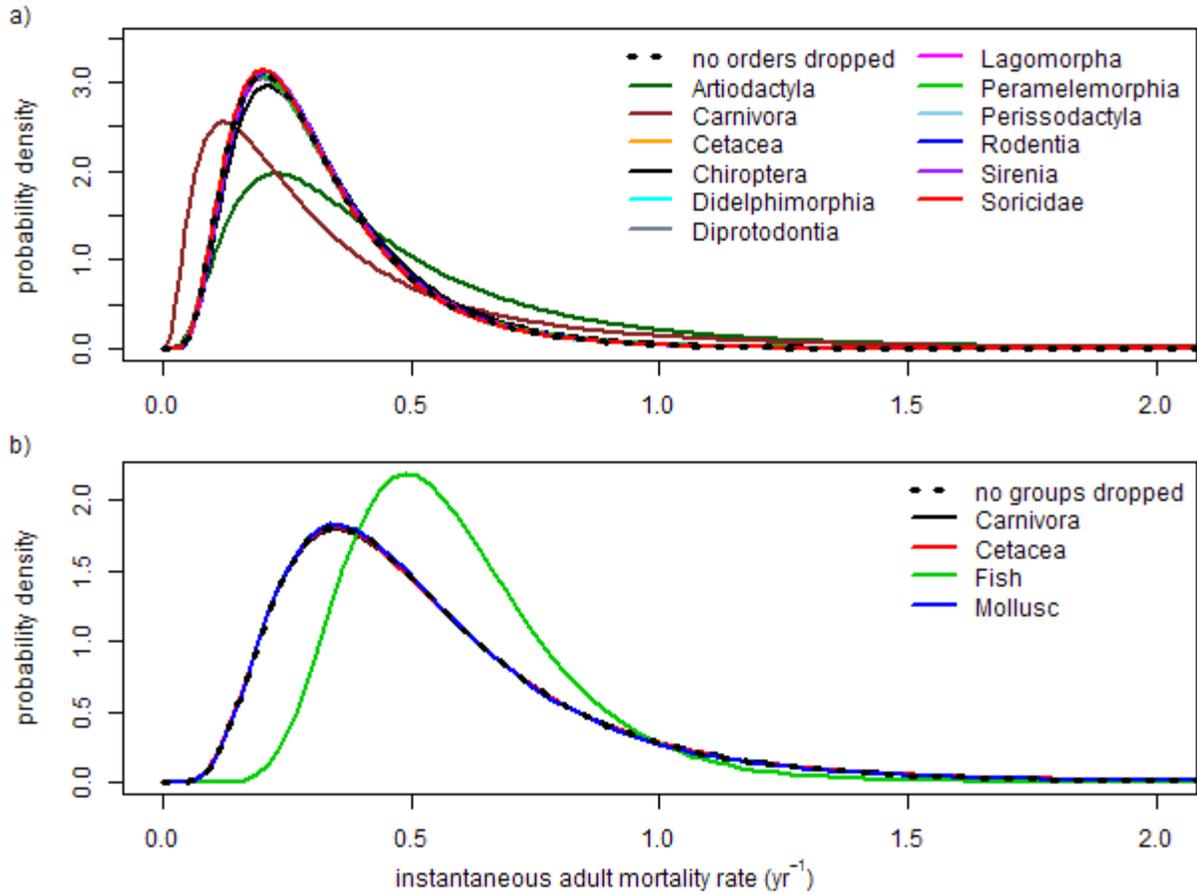


Figure 5.9. Posterior probability distributions of predicted natural mortality rate for red foxes obtained from sensitivity analyses using a) the McCarthy model, and b) the Hoenig model. To determine the influence of each taxonomic order/group, the analysis proceeded with data from each of the orders/groups dropped sequentially. The legend indicates which order/group was dropped in each analysis.

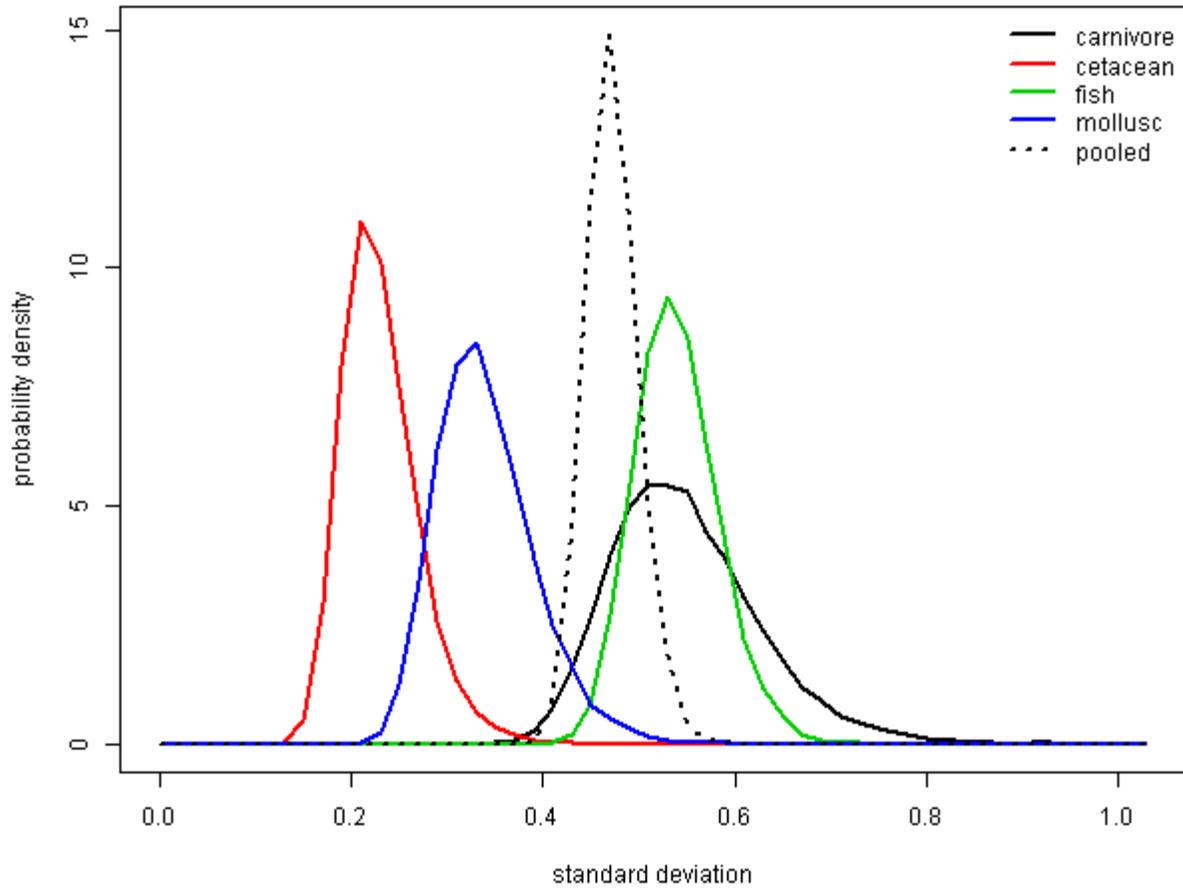


Figure 5.10. Posterior probability distributions for the standard deviation in $\ln(Z)$ deviates from a model that allowed estimation error in total instantaneous mortality rate to differ between taxonomic groups compared to a model that pooled estimation error.

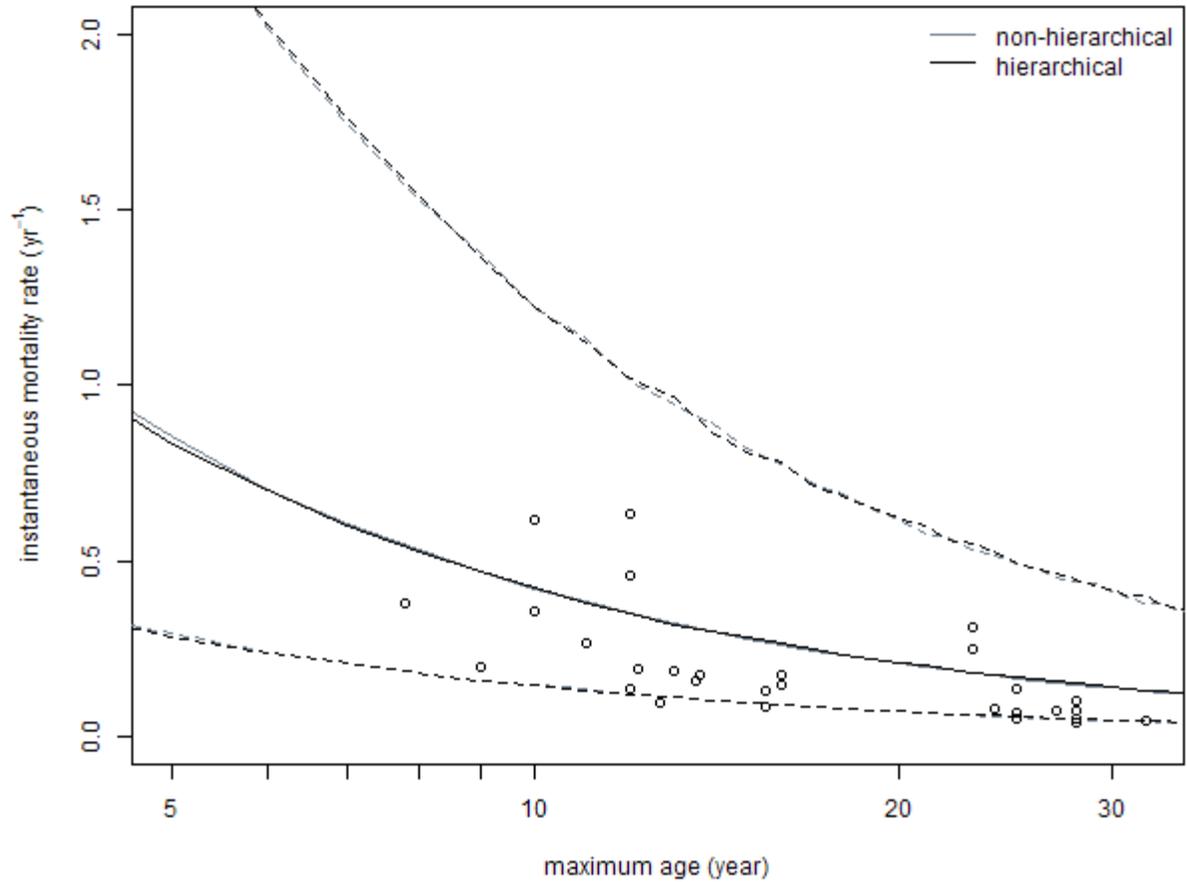


Figure 5.11. Predicted relationship between instantaneous adult mortality rate and maximum age for species within the carnivore group. Predictions are shown from analyses with both non-hierarchical and hierarchical model structures. Solid lines show the posterior median prediction and the dashed lines the 95% credible interval. Each mean mortality rate estimate from the database is shown by a circle.

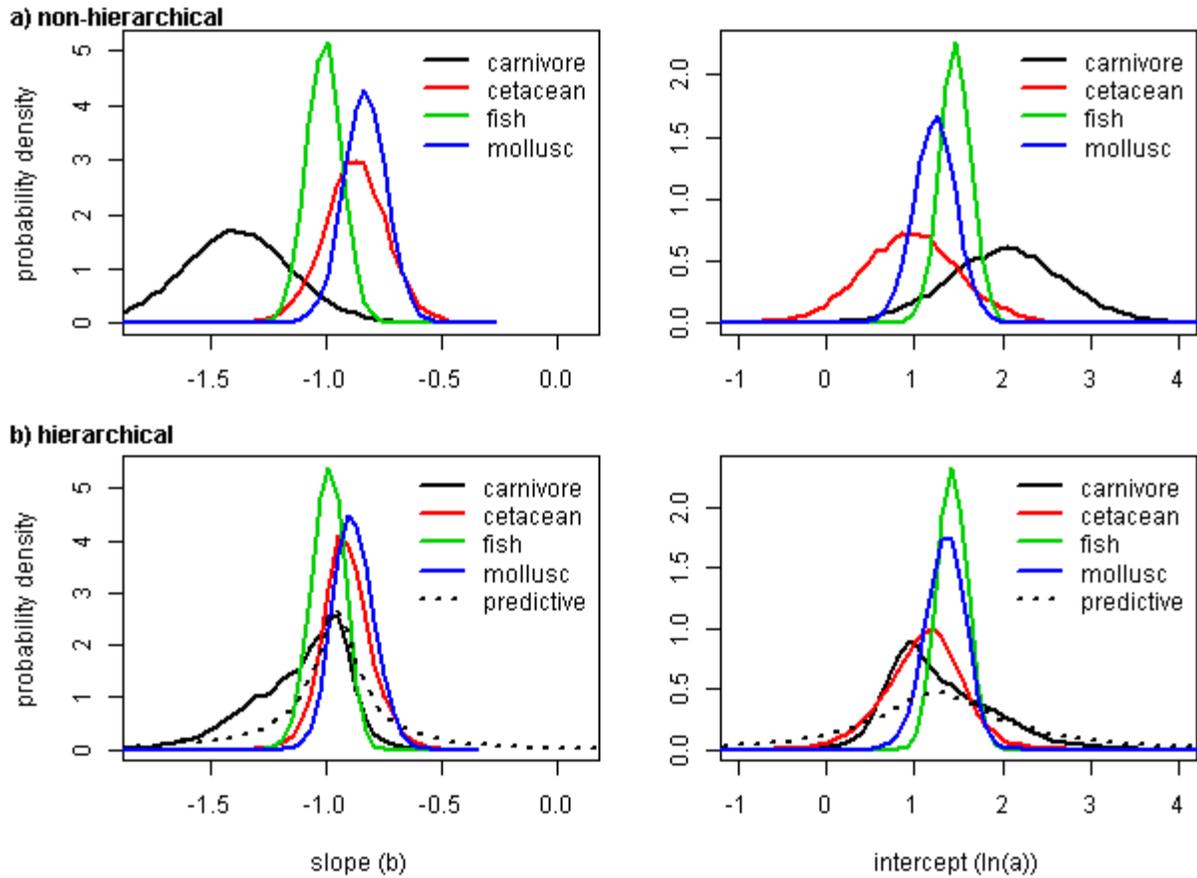


Figure 5.12. Posterior probability distributions of the slope and intercept parameters for each taxonomic group from a) a non-hierarchical model and b) a hierarchical model. The hierarchical model panel also shows the posterior predictive distribution for each parameter that is described by the hyperparameters.

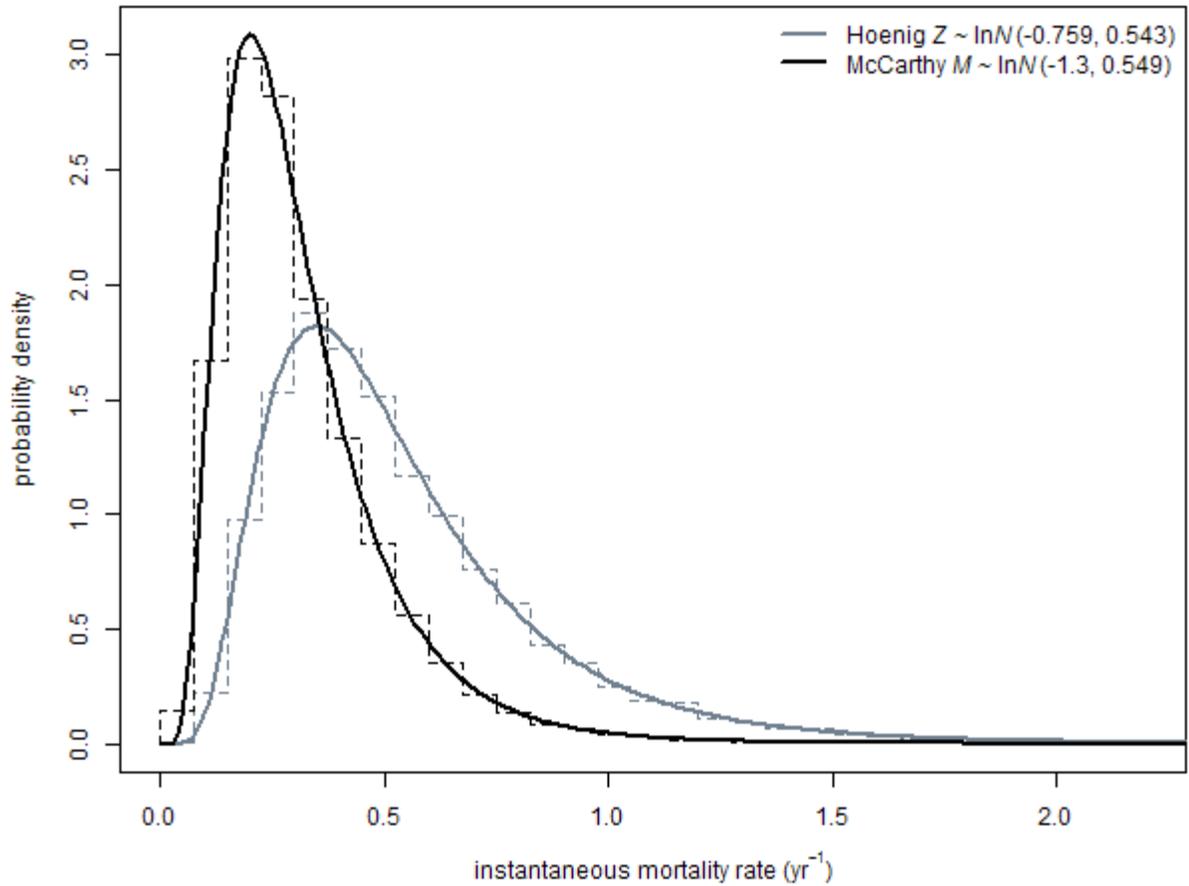


Figure 5.13. Comparison of the red fox non-culling mortality rate prior probability distributions established using the Hoenig and McCarthy models. Histograms of the posterior samples are shown by dashed lines. The legend shows the parameter values of the lognormal distribution, i.e. the mean and standard deviation of the natural logarithm of mortality rate.

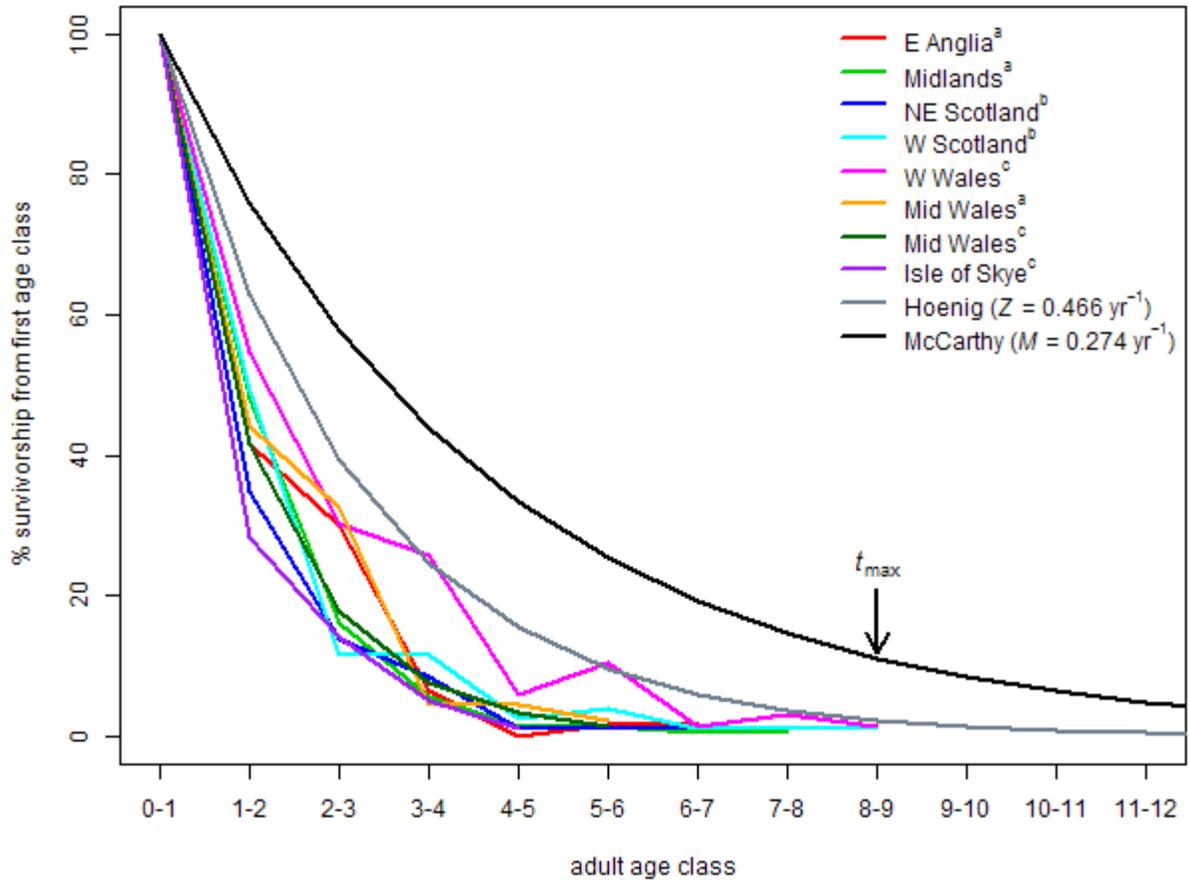


Figure 5.14. Survivorship of different rural British fox populations from observed adult age distributions, showing the comparison with the predicted survivorship that would occur if a population was under either the Hoenig or McCarthy mortality rate estimate. All fox ages were determined from incremental lines in the teeth cementum. ^aHeydon and Reynolds (2000b), ^bKolb and Hewson (1980), ^cLloyd (1980).

Chapter 6: An informative prior for the rate of successful search of foxes by gamekeepers from distance sampling data

6.1 Introduction

Relative abundance data, such as catch or sightings per unit effort, are commonly used to fit population dynamics models by directly relating relative abundance to the absolute abundance using a constant scaling parameter. A key assumption with the direct index approach is that the relationship between the relative-abundance index and population abundance is linear with zero intercept, i.e. is proportional to abundance, and that a unit of effort results in a constant proportion of the population being caught or seen, i.e. that the scaling parameter is independent of abundance (Caughley 1977; Roseberry & Woolf 1991; Hilborn & Walters 1992). Failure of this assumption can cause the model to make incorrect predictions, either because the relative-abundance index shows hyperdepletion and declines rapidly over time compared to abundance, e.g., it measures the abundance of a subset of the fox population that is more likely to be seen and therefore removed earlier; or the index shows hyperstability and stays high as abundance declines, e.g., gamekeepers are efficient at finding foxes and concentrate their efforts where foxes are most abundant, and the fox density remains stable in these areas as overall abundance declines. Violation of this assumption can therefore lead to poor estimates of abundance using relative abundance index data.

An additional parameter can be incorporated into the model to represent non-linearity between the scaling parameter and abundance. However, this often leads to model over-parameterisation and it is usually not possible to uniquely estimate this parameter without very informative data (Hilborn & Walters 1992; Walters & Martell 2004). Given that such data are rarely available, it is therefore crucial to use other insights to define the scaling parameter appropriately at the outset.

For the FMS gamekeeper lamping effort data (Chapter 2), the definition of the scaling parameter that relates sightings to the fox population is dependent upon assumptions made about the area searched by the gamekeeper during the lamping process. A discussion about

the most appropriate definition forms the first aim of this Chapter. The second aim is to establish an informative prior probability density function for the scaling parameter in the fox population dynamics model developed in Chapter 3.

6.1.1 Sightability coefficient

Some of the first models to incorporate a scaling parameter to relate counts to abundance aimed to estimate population size in closed systems (Leslie & Davis 1939; DeLury 1947); the FMS fox model is an extension of these models for open populations. The observation sub-model makes the assumption that over a time interval, e.g., one week, the number of sightings Y_t and the abundance F_t of foxes in the population are related by:

$$Y_t = qE_tF_t \quad \text{Eq. 6.1}$$

where E_t is a measurement of the sighting effort over the time interval e.g., the number of hours spent lamping, and q is the “sightability coefficient”. A unit of effort therefore results in detecting a constant proportion of the population. A summary of all model parameter and variable symbols and definitions used in this chapter is provided in Table 6.1. The sighting per unit effort I_t is the number of sightings per unit effort over the time interval and is defined as:

$$I_t = Y_t/E_t = qF_t \quad \text{Eq. 6.2}$$

Although the sighting per unit effort can be used to fit the model, it is more appropriate here to directly model the number of sightings using Eq. 6.1 as a discrete process, e.g. using the Poisson or negative binomial probability distribution. This is because the number of fox sightings on an estate over a time interval is usually small, and the data include some time intervals that have zero sightings. In these instances the effort information would otherwise be lost by fitting to sighting per unit effort. The fox model is therefore ‘conditioned’ on sightings rather than sighting rate.

The sightability of foxes is the relationship between the sighting per unit effort and the abundance in the area searched, meaning that the unit of sightability is the proportion of

the fox population in the lamped area seen per unit effort and per unit time, i.e., foxes seen per foxes available per unit effort and per unit time. It should be noted that these units differ from those of the sighting probability p , which is the probability of sighting a given fox present in the area surveyed, and therefore dimensionless.

Sighting probability (or detection probability) is frequently used in wildlife studies to correct counts of animals to produce estimates of population size (White 2005). The standard methods to estimate it are distance sampling (Buckland *et al.* 2001), mark-encounter models (Otis *et al.* 1978; White *et al.* 1982), and sightability correction models (Samuel *et al.* 1987). It is also used to correct false absences in site occupancy modeling (MacKenzie *et al.* 2006). In all of these methods, sighting probability is commonly also referred to as sightability. Although the units of sightability and sighting probability are different, the two parameters are closely related and share the same numerical value, as shown by Eq. 6.1 under the condition where the effort is equal to 1 (unit). In that situation, the number of sightings will equal the sighting per unit effort and so the sightability coefficient can be considered as the probability of any given fox being seen.

However, the relationship is not quite that simple because the sighting probability p is independent of the area searched, while the sightability coefficient q is not. The sightability definition arose in the fisheries literature as the ‘catchability’ coefficient, where it can be traced as far back as Baranov in 1918 (Arreguín-Sánchez 1996). The catchability coefficient was used in the Schaefer (1957) catch equation (from which Eq. 6.1 is derived) which relates catch per unit of fishing effort to abundance. The capture efficiency of the fish sampling gear, which is defined as the probability of capture (between 0 and 1) for a fish fully selected by the gear based upon size, is related to the catchability coefficient because:

$$q = c(a/A) \tag{Eq. 6.3}$$

where q is the catchability coefficient, c is the capture efficiency, a is the area swept by a unit of effort by the fishing gear, and A is the area of the fishing ground (Paloheimo & Dickie 1964). The efficiency can therefore only equal the catchability if the entire fishing ground is swept. This highlights an implicit assumption that a is also the area swept by one unit of

fishing effort (Thorarinsdóttir *et al.* 2010). Given that the efficiency is analogous to the sighting probability, Eq. 6.3 can be interpreted in terms of the lamping data as a is the area searched by the gamekeeper, and A is the estate area. The sightability coefficient is therefore the sighting probability scaled by the proportion of the estate area searched, with the constraint that a can be searched using one unit of lamping effort. Without information on the area searched by the gamekeeper, the precise nature of the relationship between the parameters will therefore be unknown.

The probability of sighting a fox at any time depends on several factors which include: 1) fox availability in the searched area; 2) fox behaviour towards the lamp; 3) the age/size of the fox; 4) the habitat being searched; 5) the weather conditions during the search effort; 6) the quality of equipment, e.g., lamp power; and 7) the experience of the gamekeeper. The sightability coefficient is therefore a complicated factor. As information on these possible causes of variation in sightability is usually lacking, these factors are assumed to be invariant of abundance, time, age/size, and individual skills of the gamekeeper. Sensitivity of results to potential variations in these factors may be evaluated. It is also an assumption that a shot taken at a sighted fox does not affect the behavior of nearby foxes. Making these rigid assumptions allows sighting per unit effort to be considered directly proportional to abundance and be used as an index of relative abundance.

In the fisheries literature, where this theory originated, the population is usually expressed in units of biomass or numbers of a fish stock inhabiting some defined area. This is in contrast to terrestrial systems, where the population is usually expressed as a density. Densities are especially useful when the goal is to compare population statuses among sites of different size, e.g., estates across Britain. This requires modification of Eq. 6.1 to account for the area searched in order to predict the number of sightings over a time interval. Unfortunately, the area searched over a time interval by a gamekeeper on an estate is generally not known; this is true of the FMS data.

Consideration of the search behaviour of a gamekeeper when lamping on an estate can allow assumptions to be made about the area searched. The lamping (or spotlighting) method takes place by the gamekeeper scanning the area with a high-powered spotlight to

search for fox eyeshine, either from the back of a vehicle with a driver, from a quad bike, or on foot. Once a fox is seen, the gamekeeper will attempt to shoot the fox if the distance is close enough to ensure a successful shot and if there is a safe backdrop in case of a missed shot. When searching, the gamekeeper will travel at a relatively constant speed, but will stop to 1) make use of good viewing locations, e.g., gaps in hedgerows, 2) confirm animal identification, 3) attempt to call distantly sighted foxes within shooting range, and 4) take shots at foxes (Bucknell 2001). Gamekeepers are typically responsible for the fox control across an entire estate and will aim to keep the fox population low throughout its area. However, it is not reasonable to assume that the total area searched by one unit of effort is equal to the estate area, as the actual area searched may be either more or less than the estate area and there is no means of knowing this from the FMS data. The choice of the sightability coefficient as a definition of the scaling parameter is therefore inappropriate.

6.1.2 Rate of successful search

An alternative approach to calculating the number of sightings from the density of foxes is to model the detection process using the predation mechanics theory behind the Holling disc equation (Holling 1959a). Rather than making an assumption about the area searched this approach directly estimates the area searched from theory. Given the absence of a clear linear relationship between the mean number of hours lamping per week and estate area (Figure 6.1), as might be expected if the gamekeeper searches an entire estate, this seems sensible. Starting by classifying gamekeepers as predators and foxes as prey, an individual gamekeeper's search path can be described as if they were a moving disc with radius r , i.e. the gamekeeper can search for foxes in a two-dimensional field of view of diameter $2r$ around them (Figure 6.2). The radius of this field of view will depend both on the ability of the gamekeeper to detect foxes and on the visibility of the foxes themselves, which makes it likely that the field of view would be habitat dependent. The area searched by the gamekeeper then becomes a function of their field of view, speed of travel, and the time spent searching:

$$a = 2rvE_t \tag{Eq. 6.4}$$

where v is the speed at which the observer travels, making the search rate equal to $2rv$. The area searched by the gamekeeper is therefore the hatched area in Figure 6.2. Assuming the foxes were randomly distributed across the estate, the number of foxes seen would therefore simply equal the area searched multiplied by the fox density:

$$Y_t = aN_t \quad \text{Eq. 6.5}$$

However, not all foxes available to be seen within the area searched at any time will be seen by the gamekeeper due to the factors described above, which requires that the sighting probability be introduced on the right-hand side of Eq. 6.5. For notational simplicity, p , r and v are combined into a single constant, d , the rate of successful search (Holling 1965):

$$d = p2rv \quad \text{Eq. 6.6}$$

This then gives the expression for the number of foxes seen used in Chapter 3:

$$Y_t = dE_tD_t \quad \text{Eq. 6.7}$$

While similar to the sightability coefficient as defined above, the rate of successful search is instead defined as the effective area swept per unit of time spent searching [unit check: number = (area/time)(time)(number/area)]. The rate of successful search has been defined elsewhere as the encounter rate, expressed as the number of foxes seen by a gamekeeper per unit fox density per unit time (Case 2000), but these units are more complicated. The rate of successful search will be equal to the sightability coefficient if the area searched is equal to the entire estate area. As the rate of successful search also incorporates the probability of sighting a fox, it will depend upon the same factors as sightability. As for sightability, it is assumed that the rate of successful search is invariant to these factors as information on the possible causes of variation in them is usually lacking.

By removing the need to directly incorporate the area searched into the equation for the number of fox sightings, the predation mechanics approach becomes a better option compared to assuming the entire estate area is searched over a time interval, which does not

seem valid for foxes on British estates. Compared to the sightability coefficient, the rate of successful search is therefore a more appropriate choice of definition for the scaling parameter in Eq. 6.1. It does however make the implicit assumption that the gamekeeper searches at a constant speed, an assumption that is probably invalid as few gamekeepers are constantly moving when searching for foxes. Whether using a vehicle or on foot, they will stop at locations that give better views or to try and call sighted foxes within shooting range. The amount of time spent not moving will depend on each gamekeeper's individual preferences on how to lamp over the habitats on their estate. In addition, gamekeepers must stop to attempt to shoot sighted foxes and so it is assumed that no substantial time is lost from searching when each fox sighted is shot. These stoppages will affect the average search speed if the movement of foxes was not random ahead of the gamekeeper. These movements may be affected if foxes become scared following hearing a shot nearby.

The linear relationship between fox sightings and fox density in Eq. 6.7 results in a Type 1 functional response (Holling 1959b). The alternatives to this would either be the curvilinear Type 2 (hyperbolic) or Type 3 (sigmoidal) functional responses which are asymptotic – there is a limit to the number of foxes that can be sighted per unit time at a given fox density. These relationships require additional parameters to describe them, such as the amount of time it takes to kill a fox, i.e., the handling time. It can therefore be seen that the linear relationship assumption essentially means that the handling time is assumed to be zero.

Given that the time taken to sight and shoot at a fox will on average be the same whether the shot is successful or not, the total handling time is related mainly to the number of foxes killed, as time will only be allocated to collecting foxes for sex or age determination if the shot is successful. In the FMS, sex and age data were available for only 12% of foxes shot (Chapter 2). Some gamekeepers could have collected foxes but not submitted body parts for analysis, e.g. they couldn't be bothered or had no freezer to store them in, but the data suggest that the majority of gamekeepers don't collect foxes shot when lamping, and so the average handling time for this dataset could be assumed to be minimal. It therefore seems reasonable to assume that the search time is approximately equal to the total lamping

effort for these data, leading to Eq. 6.7. If this was not the case, e.g. if each shot taken scares away nearby foxes to effectively make the search path shorter, the total sighting effort can be allocated into search time and handling time using the Holling disc equation (Holling 1959a). This requires that assumptions about the average handling time and that it is constant across gamekeepers are made, or for handling time to be estimated from the sighting data. A full derivation of this equation in the gamekeeper and fox system is given in Appendix A. The assumptions of constant density and random search behind this derivation and the use of the rate of successful search parameter are examined in Appendix B and Appendix C.

6.1.3 Distance sampling

Estimates of the rate of successful search for foxes can be obtained by using Eq. 6.1 together with results from an analysis of data from distance sampling, which is a method used to estimate the abundance and/or density of animals in a survey area (Buckland *et al.* 2001). Distance sampling involves surveying a set of line or point transects laid out within the survey area and for each sighting, the perpendicular distance from the transect to the animal is recorded. The distribution of distances is used to estimate the detection function $g(x)$, which describes the probability that a fox at distance x from the transect is detected. The detection function is then used to estimate the average detection probability over the surveyed strip, allowing the number of animals detected to be scaled up to the number of animals present (for detailed information see Buckland *et al.* 2001). Distance sampling has previously been used to estimate density of foxes in rural European landscapes (Heydon, Reynolds & Short 2000; Ruelle, Stahl & Albaret 2003). As the survey procedure used in these studies is comparable to a gamekeeper lamping, with sampling performed from vehicles driven along roads or tracks using a spotlight to detect fox eyeshine, the rate of successful search when lamping on an estate can reasonably be assumed comparable to the rate of successful search estimates observed during these distance sampling studies. Such estimates can be used in combination with expert judgment to establish an informative prior probability distribution for d to use in Bayesian population dynamics models, following

approaches used in the fisheries literature to formulate prior probability density functions for catchability (McAllister, Stanley & Starr 2010).

6.2 Methods

There are two main steps in the procedure for computing a prior probability density function for the rate of successful search: 1) establish a conceptual prior using Monte Carlo simulation and knowledge about the component factors of the rate of successful search (sighting probability, search speed, and field of view radius); and 2) update the conceptual prior using empirical estimates of d from distance sampling studies. The posterior predictive distribution from this analysis can then be used as a prior probability density function for d on any given estate.

6.2.1 Specification of a conceptual model for the rate of successful search

In describing the search process above, the rate of successful search has been shown in Eq. 6.6 to be the product of the sighting probability p , the radius of the observer's field of view r , and their speed of travel v . Each of these multiplicative factors can be assigned a probability distribution; by then using a Monte Carlo approach to simulate values from each of the factors a probability density function for d can be established using Eq. 6.6. As the factors are multiplicative, the resulting prior for d can be approximated by a lognormal random variable. Two alternative prior distributions were considered for each of the rate of successful search factors, one that was non-informative and one that was more informative based upon empirical data or expert judgment. This resulted in eight candidate conceptual distributions with contrasting levels of information on d . The parameterisation of each of the factors is described below.

6.2.1.1 Sighting probability

Sighting probability was described using a beta distribution with parameters a and b

$$p \sim \beta(a, b)$$

For the non-informative distribution, it was assumed that $a = b = 1$ to give a uniform distribution on the $[0, 1]$ interval. The informative distribution was parameterised using the estimates of p obtained from the distance sampling analysis (see 6.3.1). Maximum likelihood was used to fit a beta distribution to these p estimates by using the ‘fitdistr’ function of the MASS package (Venables & Ripley 2002) within the R statistical software (R Core Team 2013). The fitted a and b values determined the informative beta distribution.

6.2.1.2 Field of view

The uniform distribution with parameters a and b was used to describe the field of view radius such that

$$r \sim U(a, b)$$

For the non-informative distribution, it was assumed that a was equal to 0.01 km and b was equal to 0.75 km. This represents a range from being able to see foxes only if they are very close, e.g., due to dense wooded areas, high hedgerows adjacent to the road, or poor visibility due to weather; up to a maximum distance a fox can correctly be identified by eyeshine, e.g., when the land is flat and there is excellent visibility. For the informative distribution, the minimum value was assumed to be the same (0.01 km) but the maximum value was obtained from the maximum observer-to-fox distance (not perpendicular distance from the transect) from the distance sampling data.

6.2.1.3 Speed of travel

As described above, the speed of travel represents an average search speed that will be somewhat dependent upon the amount of time a gamekeeper spends not moving, which varies between individuals. For the non-informative distribution, the uniform distribution with parameters a and b was used to describe the speed of travel such that

$$v \sim U(a, b)$$

It was assumed that a was equal to 1 km hr⁻¹ and b was equal to 30 km hr⁻¹ giving a range that would encompass gamekeepers who walk and stop frequently to those who use a vehicle

and stop infrequently. The informative distribution was parameterized using data on the speed that transect sections were traversed during distance sampling surveys (see 6.3.1). Maximum likelihood was used to fit a lognormal distribution to these v estimates, with the fitted values used to determine the informative lognormal distribution.

6.2.1.4 Monte Carlo simulation

The conceptual prior distribution for the rate of successful search was obtained by synthesizing the inputs to Eq. 6.6 using a Monte Carlo simulation method. A single simulation involved drawing random numbers from each of the distributions of sighting probability, speed of travel and field of view to give a value for d under the various priors for each factor. The conceptual prior distribution for d was determined from a total of 1,000 simulations using WinBUGS 1.4 (Spiegelhalter *et al.* 2007), implemented from within R using the R2WinBUGS package (Sturtz, Ligges & Gelman 2005). This gave 8 alternative prior distributions for d based upon different amounts of knowledge on each factor. These were used for a sensitivity analysis to determine the influence the conceptual prior had upon the posterior predictive distribution obtained by updating the priors with the estimates of d from distance sampling.

6.2.2 Estimation of the rate of successful search from distance sampling data

6.2.2.1 Survey procedure

The study by Heydon *et al.* (2000) used driven line transects to estimate densities of fox, badger and hare in 3 large (626 to 1458 km²) regions of Britain: a) mid-Wales, b) east-Midlands, and c) East Anglia. Surveys were carried out at night using spotlights during autumn 1995 and 1996, and spring 1996 and 1997. In each region, 160-180 km of minor public roads were selected as the transect route and aimed to provide thorough coverage of each region. The vehicle, a Toyota Hilux, was driven at between 15 and 25 km h⁻¹, slowing down and stopping at gaps in hedges as necessary. Surveys were carried out by 2 people (1 driver and 1 observer) who exchanged places every hour; no observer effects were found in ability to detect foxes. The observer stood on a raised platform mounted on the back of the

vehicle and scanned fields on the left side of the road with a hand-held, 1-million candle-power halogen spotlight. Both observer and driver also scanned the road direction ahead.

The perpendicular distance of each animal sighting location from the centre of the road line was visually estimated by the observer with the aid of binoculars and 1:25,000 scale topographic Ordnance Survey maps, giving details of field boundaries and other landscape features. Transects were repeated up to four times over ten days to ensure enough sightings for reliable density estimation. Half of each transect route (a transect section) was surveyed during a single night, with the start point varied such that individual sections were surveyed at different times. Surveys were carried out between 20:00 and 06:00 and the total time taken for each transect section was recorded.

6.2.2.2 Density estimation

The original sighting data from Heydon *et al.* (2000) were used to estimate fox density of foxes in each region (a, b, c), study year (1995-96, 1996-97) and season (autumn, spring) using program Distance 6.0 release 2 (Thomas *et al.* 2010). The reanalysis of the data was necessary to enable the estimation of sighting probability for each region and season combination, as these values were not reported in Heydon *et al.* (2000). As in Heydon *et al.* (2000) the data were grouped into intervals of 50 m to improve estimator robustness due to evidence of heaping (Buckland *et al.* 2001). Data were then right-truncated to the interval at distance w to remove outliers such that $\hat{g}(w) \approx 0.15$ (Buckland *et al.* 2001). The truncation distances were not reported in Heydon *et al.* (2000) but varied depending upon region and time of year. Due to the potential for a non-random distribution of foxes near roads, i.e., the area closest to the road may be avoided, left truncation of the data at 10 m was considered to produce improved estimates that would be more representative of the survey region (Buckland *et al.* 2001).

For each region, the detection function was pooled across study years and estimated separately for each season as it was assumed factors affecting fox detection would be constant across years. A density multiplier of 0.5 was specified to account for the use of one-sided transects (Buckland *et al.* 2001). Alternative detection function models considered

were half-normal, uniform and hazard-rate key functions with cosine adjustments, which were constrained to be strictly monotonically non-increasing. Akaike's Information Criterion (AIC) was used to select the model (key function and number of adjustment terms) that best fitted the data. The fit of models to the data was assessed using χ^2 goodness-of-fit tests and visual inspection of the distance frequency histograms, with the strength of the fit being used to guide the choice of right-truncation distance and whether to use left-truncated data. The variance of the density estimates was calculated by assuming the distribution of observations was Poisson, i.e., the foxes were distributed randomly with no aggregation. The density estimates were compared to those obtained by Heydon *et al.* (2000), small differences were expected due to choices about truncation distance and the effect of using an updated version of the analysis software.

6.2.2.3 Empirical distribution of the rate of successful search

In total 69 transect sections were surveyed to provide data for use in calculation of the observed rate of successful search. The rate of successful search on each transect section was estimated by rearranging Eq. 6.7 and substituting the time taken to survey a given section for the search time, the number of foxes sighted on the section, and the estimated regional fox density during the corresponding survey period. The observed d on transect section i was considered a lognormal random variable

$$d_i \sim \text{lognormal}(\ln(d^{med}), \sigma^2) \quad \text{Eq. 6.8}$$

where d^{med} is the median for the lognormal density function for the rate of successful search, and σ is the standard deviation in the natural logarithm of estimates of d .

6.2.3 Obtaining the posterior predictive distribution

The conceptual prior and empirical estimates of the rate of successful search were integrated to obtain the posterior predictive distribution (Gelman *et al.* 2004) for use in population dynamics modelling. WinBUGS was used to apply Bayes rule and update the conceptual prior density function with the empirical data and obtain posterior density functions for the median of d and the standard deviation in the natural logarithm of the

estimates of d . These posteriors were then used in Eq. 6.8 to obtain the lognormal posterior predictive distribution for d . The prior for the standard deviation in the natural logarithm of the d estimates was assumed to be uniformly distributed between 0 and 10.

Samples of the posterior distribution of the parameters were obtained using Markov chain Monte Carlo (MCMC) methods, with an initial burn-in of 10,000. In the Markov chains, some parameters showed strong autocorrelation. To reduce the problem only 1 in 100 iterations were recorded. Inferences were then derived from a sample of 50,000 iterations from two chains of 25,000 iterations. Convergence of these samples to the posterior distribution was assessed using the CODA package (Plummer *et al.* 2006) in R by examination of two independent Markov chains and calculating the Gelman-Rubin convergence diagnostic (Gelman *et al.* 2004). When this value became <1.01 , the chains were assumed to have converged.

6.3 Results

6.3.1 Conceptual priors

Pooling the detection functions across study years in each region meant that there were only 6 independent sighting probability estimates obtained from the best fitting distance sampling models. These had an overall mean of 0.531 (range 0.410-0.679). The regional means were 0.453 (Wales), 0.597 (Midlands) and 0.544 (East Anglia). The seasonal means were 0.505 (autumn) and 0.558 (spring). Fitting a beta distribution to all 6 values gave estimates of a and b of 18.56 and 16.34, respectively, resulting in an approximately symmetrical distribution around the mean value (Figure 6.3a).

The mean speed that transect sections were traversed at when surveyed was 15.2 km hr⁻¹ (range 10.0- 24.3 km hr⁻¹). This mean speed estimate included time that was spent stopped, e.g. at gaps in hedgerows. The values appear to fit a lognormal distribution (Figure 6.3b). The maximum distance from an observer of a sighting that was reliably identified to be a fox from the line transect survey was 500 m. The two foxes sighted at this distance were both seen on land classified as fertile coastal plain. This land class, being predominantly flat, offered excellent visibility when weather conditions were good.

The differences between the conceptual priors for the rate of successful search are shown in Table 6.3. All showed the expected lognormal distribution. The amount of information in the prior distribution of each factor caused large differences in the median values, which ranged from 1.84 to 4.65 km² hr⁻¹. However all the conceptual priors for d were imprecise and had a CV greater than 0.85. The precision of the conceptual prior was determined mainly by the amount of information contained in the prior for the sighting probability factor, as shown by the differences in CV between priors a-d and e-f (Table 6.3).

6.3.2 Distance sampling

The detection functions fitted to line transect data are shown in Figure 6.4. For each region and season combination, left truncation at 10 m was applied as this resulted in higher P -values from χ^2 goodness of fit tests compared to no left truncation, which resulted in poor fits. Right truncation distances varied between regions, but were greatest for spring transects. The fox density estimates for each region and season combination are shown in Table 6.2. The density estimates were all within either 0.05 fox km⁻² or 10% of those obtained by Heydon *et al.* (2000). Consistent with Heydon *et al.* (2000), there was large regional variation in density (Midlands > Wales > East Anglia) and autumn densities were found to be higher than those in spring. From these density estimates, the rate of successful search for foxes was estimated for each transect section (Figure 6.5). The estimates of d had a median value of 2.056 and a CV of 0.660.

6.3.3 Posterior predictive distribution

The empirical estimates of the rate of successful search from distance sampling resulted in a significant posterior update to all of the conceptual priors for d (Table 6.3). The results discussed further are from the analysis using the least informative conceptual prior (prior a). This prior was chosen as the sensitivity to the choice of conceptual prior, based upon the posterior predictive median values, was low (Table 6.3), but also as examination of the posterior distributions for r and v indicated that for the more informative priors the marginal posteriors for these factors were being truncated by the narrower uniform bounds placed on their priors. This affected the posterior correlations. The posterior predictive

distribution for d was also similar if a uniform prior was placed directly on d (data not shown).

The posteriors of the factors that formed the conceptual prior were updated by the distance sampling data in comparison to their priors. Sighting probability had a posterior mean of 0.455 with a 95% credible interval of [0.073, 0.962], a decrease from the prior mean of 0.500. The radius of the observer's field of view had a posterior mean of 0.330 km with a 95% credible interval of [0.053, 0.717], a decrease from the prior mean of 0.378 km. This credible interval included the greatest distance at which a fox was recorded as being sighted during distance sampling (0.688 km), but which was not deemed to be a reliable identification. The speed of travel had a posterior mean of 13.23 km h⁻¹ with a 95% credible interval of [2.16, 28.87], a decrease from the prior mean of 15.53 km h⁻¹. The posterior correlation coefficients between d and the factors forming the conceptual prior were all low (< 0.1). Pairwise correlations between p , r , and v were higher and negative, with all coefficients higher than -0.4.

The posterior distribution for the median rate of successful search was precise (Figure 6.6a), with a mean of 1.999 km² h⁻¹ and a 95% credible interval of [1.769, 2.252]. The standard deviation in the natural logarithm of the estimates of d was also precisely estimated (Figure 6.6b), with a mean of 0.510 km² h⁻¹ and a 95% credible interval of [0.434, 0.610]. The lognormal posterior predictive distribution (Figure 6.7) had a median value of 2.009 km² h⁻¹ and a CV of 0.556 (mean = 2.282, a standard deviation = 1.269).

6.4 Discussion

Predator-prey relationships, and the arguments used to derive functional response models to describe them, e.g., the Holling disc equation (1959a, 1965), have been widely applied to human interactions with harvested or culled species. Examples include in understanding the response of deer hunters to declining deer density (van Deelen & Etter 2003), evaluating shooting of feral pigs from a helicopter (Hone 1990; Choquenot, Hone & Saunders 1999), and predicting catch rates by examining vessel time budgets (Hilborn &

Walters 1992). There has not been a similar study to examine the relationship between the sighting rate of foxes by gamekeepers and fox density.

The ability to model fox population dynamics using relative abundance indices such as fox sighting rate depends upon assumptions made about the functional relationship between the index and absolute density. Two key assumptions must be made about 1) the shape of the relationship, and 2) the definition of the parameter(s) that determine the relationship. To enable the use of gamekeeper lamping data to model fox populations, the number of foxes seen by a gamekeeper per unit time is assumed here to be linearly related to fox density. As density increases, the number of foxes shot should increase unless gamekeepers get to shooting saturation where more animals are seen than can be shot and hence the effect of initial density should be curvilinear, as has been shown to be the case for feral pigs (Hone 1994). This is not usually a problem for foxes, as the sighting rate is relatively low.

The linear relationship also assumes that the handling time is minimal, an important assumption as if the handling time is significant, the sighting rate is not a good index of abundance (Rist *et al.* 2008). In such situations an alternative functional response is required that incorporates handling time. For harvested species, such as deer, where there is a strong incentive to recover shot animals because the meat is required for processing, the time constraint associated with killing an individual deer is a close representation of the handling time responsible for the shape of the Type 2 functional response (van Deelen & Etter 2003). For harvested species, and many culled species, this is usually true, but is not the case for foxes and provides a reasonable argument for why the handling time for foxes would be short, as given the time it takes to take a shot once a fox is seen, the handling time for foxes equates to their collection for sex determination. The FMS data suggests that few foxes are actually collected for this purpose, i.e., gamekeepers are in general not interested for their records, so the handling time can be assumed to be minimal.

That the linear assumption is not a major issue for foxes is further supported by Figure C.2, showing a Type 2 curve parameterised using biologically reasonable values with a given handling time (0.2 hr fox^{-1}). In the relatively narrow range of densities in which rural

foxes are found in Britain (1-2 fox km⁻²), the relationship appears to remain linear as the non-linearity occurs at higher fox densities when search time is reduced by the number of foxes being killed and collected. Obviously with a longer handling time than used in this example, non-linearity will occur at lower densities, but a longer handling time than this does not seem to be usual for foxes.

This linear relationship is determined by only one parameter, the scaling parameter, which must be estimated from the data. The scaling parameter relating the fox sighting rate to fox density is shown to be correctly defined as the rate of successful search d from predation mechanics theory (Holling 1965), and has units of effective area searched per hour. This definition enables the number of sightings to be predicted from the fox density and number of hours spent lamping; an estimate of the parameter is then obtained by fitting the predicted sightings to the observed sightings. The assumptions made in using the rate of successful search, such as density being constant during the lamping period, have been shown to hold when applied to foxes as the kill rates are relatively low. However, this may not be true for all species, so the assumptions must be examined carefully for each one.

The rate of successful search is described as a product of component factors that determine the search process. These factors are: 1) the probability of sighting a given individual fox, 2) the field of view of the gamekeeper, and 3) average speed of a gamekeeper moving across the search area, i.e., estate. These factors were combined using a Monte Carlo method to establish a conceptual prior for the rate of successful search that could be updated by empirical data from distance sampling to obtain a posterior predictive distribution (Gelman *et al.* 2004) for use as an informative prior in Bayesian fox population dynamics models. In complex systems such as fisheries, such component calculations based upon chaining together assumptions perhaps do not have much meaning at field scales when the search process (and resulting prey sighting rate) is greatly complicated by prey behaviours, diurnal changes in search conditions, e.g., light, and time-allocation decisions by individual predators, e.g., short feeding bouts to avoid predation risk (Walters & Martell 2004). In comparison, these complications are relatively small in the simpler fox-gamekeeper system, with the main issue being whether foxes become averse to spotlights following repeated

exposure, i.e., lamp-shyness, or if gamekeepers show markedly different lamping behaviours. However, the estimates obtained in this way will at least give reasonable bounds on the rate of successful search (Walters 1986).

The conceptual prior distribution showed quite large differences depending upon the assumed distributions of the factors comprising it. The dominant factor was sighting probability, as highlighted by the improvement to the precision of the d estimate obtained by using a more informative distribution on sighting probability. The use of informative distributions on the other factors made little difference to the prior precision. The higher posterior correlations between the factors might have been expected given that conceptual prior was formed simply as the product of the factors, but as there was no correlation between the priors for the factors, alternative explanations were sought. The correlation between search speed and sighting probability (-0.413) can be explained by the optimal search rate or stare duration hypotheses (Gendron & Staddon 1983; Guilford & Dawkins 1987; Endler 1991). Based on observations that cryptic prey required longer viewing times before they are sighted compared to less cryptic prey, these hypotheses intuitively state that if a predator increases its mean viewing time within a search area by reducing the search speed and taking longer stares at each stop, it will increase the probability of sighting more cryptic prey. The correlation between field of view and sighting probability (-0.401) can be explained by the notion that if the field of view is narrower, the sighting probability is likely to be higher compared to if the field of view is wider. The correlation between field of view and speed of travel (-0.426) suggests that there is not enough information in the data to choose between scenarios where a narrower search path was traversed faster or where a wider search path was traversed slower as both were equally likely.

The imprecision of even the most informative conceptual prior meant that the posterior predictive distribution for the rate of successful search was determined mainly by the empirical estimates from distance sampling. This was highlighted by placing a uniform prior directly on d rather than using the conceptual prior for d , which produced similar posterior estimates of d to those obtaining using the conceptual prior. This is possibly indicative of an oversimplification of the search process in deriving the conceptual prior. It

must be noted that use of information on the sighting probability obtained from distance sampling to form the conceptual prior for d is subject to criticism as this prior is then updated with empirical estimates of d from the same distance sampling study. Although not technically the same data there is undoubtedly an element of circularity as sighting probability is a component of the rate of successful search; however, given the lack of influence the choice of conceptual prior had as shown by sensitivity testing, the conclusion is that it has not affected the result.

The empirical estimates for the rate of successful search from distance sampling are heavily dependent upon the reliability of the fox density estimates. Distance sampling using line transects makes several assumptions to enable representative sampling and unbiased density estimation, one of which is that transects are located randomly (Buckland *et al.* 2001; Thomas *et al.* 2010). Distance sampling using tracks will therefore be representative only of the habitat adjacent to the tracks and there may be a density gradient of foxes perpendicular to the track (Buckland *et al.* 2001; Fewster *et al.* 2008); because of this distance sampling using roads or tracks as survey routes can lead to biased density estimates for some species (Porteus, Richardson & Reynolds 2011). The density estimates should not be extrapolated across the entire survey area for these reasons, although given sufficient replication tracks can be valuable survey routes if animals are randomly distributed with respect to the tracks (Venturato, Cavallini & Dessì-Fulgheri 2010). For these survey data, there is no reason to assume that foxes would avoid the habitat adjacent to tracks, especially where these are not major roads. For calculation of the rate of successful search, the density in the area around the tracks is actually what is required because this is where lamping takes place, so this is not an important issue. In any case, an additional check on the reliability of the density estimates obtained by distance sampling was that they were similar to those obtained using breeding earth censuses (Heydon, Reynolds & Short 2000).

The speed of travel along each distance sampling transect was used to inform the conceptual prior for the gamekeepers speed of travel factor. This speed ranged widely between transects (10.0 to 24.3 km h⁻¹). Each transect followed the same sampling protocol, but different combinations of observers were used for each one. Heydon *et al.* (2000)

examined the effect of observer on sighting rate (not significant) and on perpendicular distance estimates (only significant during spring in one region), but did not examine whether the speed of travel differed between observers. Some gamekeepers will stop longer at certain points on the lamping route, e.g., at hedgerow gaps, to try and sight foxes, and this may be related to observer experience. As introduced above, an implicit assumption behind the rate of successful search in the Holling disc equation is that the search is performed at a constant speed. However, few natural predators are continuously on the move when hunting prey. For example, when foxes are hunting small mammals they will usually begin by walking down a trail, and when suspecting a prey is near the trail the fox will try to locate it by stopping and either staring, sniffing, or listening (Österholm 1964; Henry 1986). This behaviour is therefore part of the search process rather than the capture process, and is analogous to a gamekeeper stopping and searching when lamping.

An important consequence of this variation in speed of travel is that it will differ on each estate due to observer behaviour but also due to habitat, e.g. woodland areas will typically be skipped through faster as reflection off leaves makes the sighting conditions poor. The field of view and sighting probability will also vary between estates. Using the right-truncation distance as a proxy for the maximum distance at which foxes could be reliably sighted, the distance sampling data showed that visibility varied between regions, indicating habitat may be important, but that visibility also appeared to be greater in the spring, suggesting seasonal variation. The distance sampling surveys took place when visibility of foxes was likely to be near-optimal depending upon weather conditions, i.e., in spring before there was any crop cover, and in autumn after harvest. The sighting probabilities estimated here are therefore likely to be higher than if the surveys were performed at other times of year.

Few other estimates of fox sighting probability were available. The only other known distance sampling study on foxes was conducted in the spring using a similar survey procedure in France (Ruelle, Stahl & Albaret 2003). Estimates of p in that study were in the range 0.53-0.76, so comparable to the mean springtime estimate in this chapter of 0.55. Another comparison comes from an occupancy model that used data from an Australian fox-

monitoring program. This suggested that p was much lower than estimated here, varying from 0.06 in the cropping season when roadside vegetation was present, up to 0.18 in the non-cropping season when roadside vegetation was absent (Field *et al.* 2005). The latter value is the most useful comparison as the time of year is similar, but differences in the survey procedure between studies must be considered. Compared to Heydon *et al.* (2000), Field *et al.* (2005) undertook their survey from within the vehicle rather than from a raised platform mounted on the back of the vehicle, drove the transects at least 5 km h^{-1} faster, and used a different spotlight (not comparable as the power of the lamp was quoted rather than the luminous intensity). All of these provide plausible explanations for why these estimates are lower than those obtained here, but the lower observation position is probably the main difference.

In the absence of covariate information on how each gamekeeper lamped on their estate, i.e., if they walk or use a vehicle, which would better inform the priors placed on speed of travel and field of view, it is necessary to estimate the rate of successful search at the estate-level as not all gamekeepers will show the same lamping behaviour as was used in the distance sampling survey. The ability to obtain seasonal estimates is desirable given the likelihood of there being seasonal differences in the sighting probability for foxes due to visibility changing, e.g., due to crop cover, but this would require the estimation of additional parameters in the fox population dynamics model.

6.4.1 Summary

This chapter provides a description of the detection process of foxes by gamekeepers using the lamping culling method. This applies the predation mechanics theory behind the Holling disc equation (Holling 1959a, 1965) to define the model parameter which scales the number of foxes sighted to the fox density as the rate of successful search. Given that the rate of successful search is the product of the search rate and sighting probability, prior probability distributions were constructed for these separate parameters that were then integrated to give alternative conceptual priors for d . Empirical estimates of d were obtained from the distance sampling data and resulting estimates of fox density. The conceptual prior and empirical estimates of d were then integrated to obtain the posterior predictive

distribution of d for use as an informative prior in population dynamics modelling. The posterior distribution was not sensitive to the choice of conceptual prior.

Assumptions of the Holling disc equation relating to: 1) constant fox density over the total search time, and 2) random search within the estate, were also examined. These analyses found that the bias in number of foxes killed by lamping which may result from failure of these assumptions was low on the average estate, unless gamekeepers had knowledge of areas with different fox density within the estate and thus did not search randomly by targeting these areas first. Most gamekeepers may be assumed not to have this knowledge of fox density and instead to simply use a lamping route that is easy to traverse and starts near to (or far away from) home.

6.5 Tables

Table 6.1. Symbols and description for model parameters and variables used in this chapter.

Notation	Description
Y_t	Number of fox sightings in time-step t
F_t	Abundance of foxes
N_t	Fox density, fox km ⁻²
E_t	Lamping effort, hr
I_t	Sightings per unit effort, fox hr ⁻¹
q	Sightability (or catchability) coefficient
p	Sighting probability
c	Capture efficiency
a	Area of estate searched (or swept by fishing gear), km ²
A	Area of the estate (or of the fishing ground), km ²
r	Radius of the observer's field of view, km
v	Speed of travel when searching, km hr ⁻¹
d	Rate of successful search, km ² hr ⁻¹
k	Probability of a sighted fox being killed
C	Number of foxes killed
E_a	Total time spent lamping, hr
E_s	Search time, hr
E_h	Handling time, hr

Table 6.2. Total survey effort, number of foxes sighted and densities of foxes estimated by line transect surveys in the three study regions, during 1995-1997. The precision of the density estimates is shown by the coefficient of variation (CV).

Region	Season	Year	Total effort (hours)	Foxes sighted	Density (foxes km⁻²)	CV
Wales	autumn	1995	26.3	29	0.76	0.205
		1996	46.4	74	0.97	0.146
	spring	1996	39.7	35	0.40	0.251
		1997	40.0	39	0.49	0.241
Midlands	autumn	1995	32.1	131	2.93	0.096
		1996	26.5	114	2.57	0.103
	spring	1996	5.8 [†]	13	0.71	0.296
		1997	29.6	74	1.02	0.136
East Anglia	autumn	1995	35.4	32	0.57	0.198
		1996	51.5	62	0.60	0.158
	spring	1996	50.4	18	0.11	0.277
		1997	49.0	25	0.16	0.240

[†]Only partial survey completed due to adverse weather

Table 6.3. Difference between rate of successful search (d) conceptual prior median and CV values under alternative distributions placed on sighting probability (p), field of view radius (r) and speed of travel (v). For each factor, these were either non-informative (flat) or informative. The posterior predictive estimates of median and CV show the sensitivity to the conceptual prior specification.

Prior	p	$r, \text{ km}$	$v, \text{ km hr}^{-1}$	$d, \text{ km}^2 \text{ hr}^{-1}$			
				Prior		Posterior	
				Median	CV	Median	CV
a	$\beta(1, 1)$	$U(0.01, 0.75)$	$U(1, 30)$	3.40	1.12	2.01	0.56
b	$\beta(1, 1)$	$U(0.01, 0.75)$	$LogN(\ln(2.71), 0.18)$	2.75	1.13	1.99	0.55
c	$\beta(1, 1)$	$U(0.01, 0.5)$	$U(1, 30)$	2.25	1.12	2.00	0.57
d	$\beta(1, 1)$	$U(0.01, 0.5)$	$LogN(\ln(2.71), 0.18)$	1.88	1.12	1.98	0.57
e	$\beta(18.6, 16.3)$	$U(0.01, 0.75)$	$U(1, 30)$	4.84	0.85	2.02	0.56
f	$\beta(18.6, 16.3)$	$U(0.01, 0.75)$	$LogN(\ln(2.71), 0.18)$	3.77	0.86	2.00	0.55
g	$\beta(18.6, 16.3)$	$U(0.01, 0.5)$	$U(1, 30)$	3.25	0.85	2.00	0.56
h	$\beta(18.6, 16.3)$	$U(0.01, 0.5)$	$LogN(\ln(2.71), 0.18)$	2.60	0.85	2.00	0.56

6.6 Figures

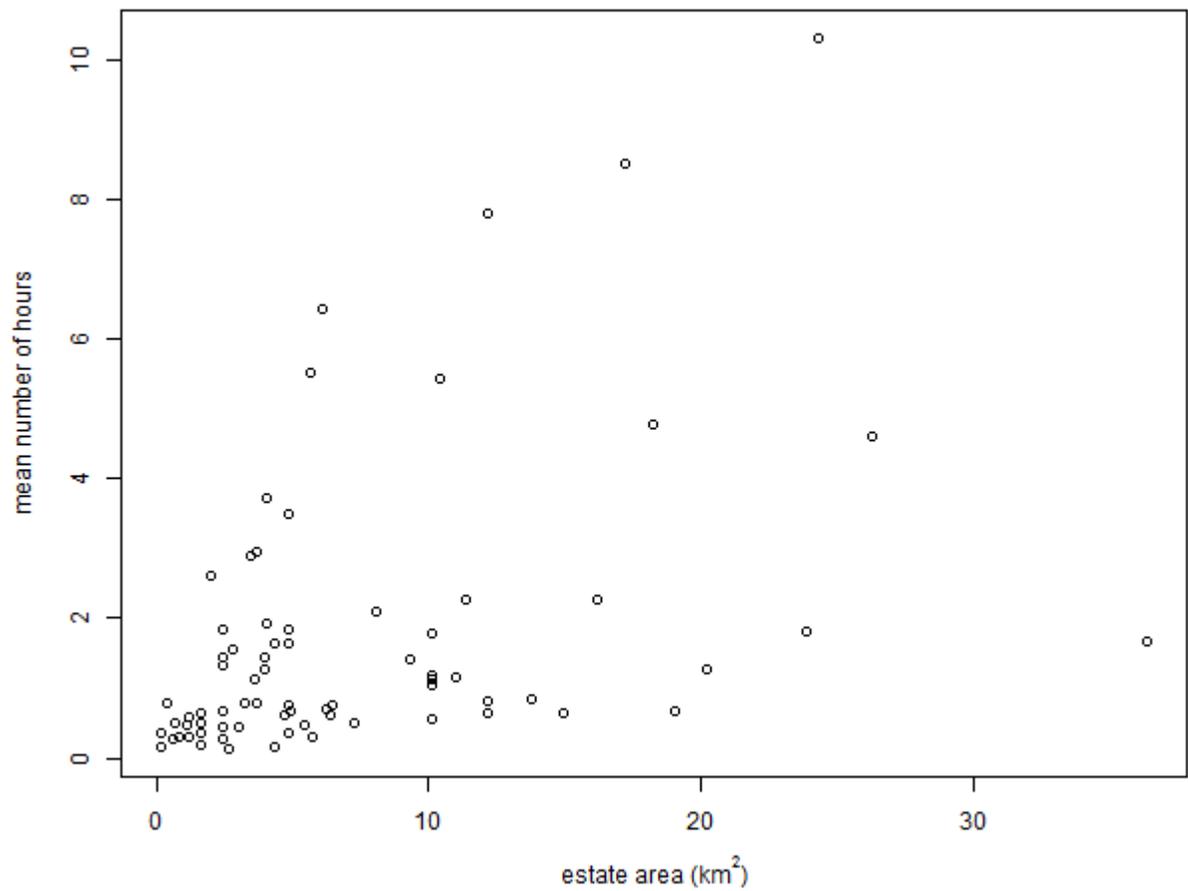


Figure 6.1. Mean number of hours spent lamping per week by gamekeepers on each of the 75 FMS estates.

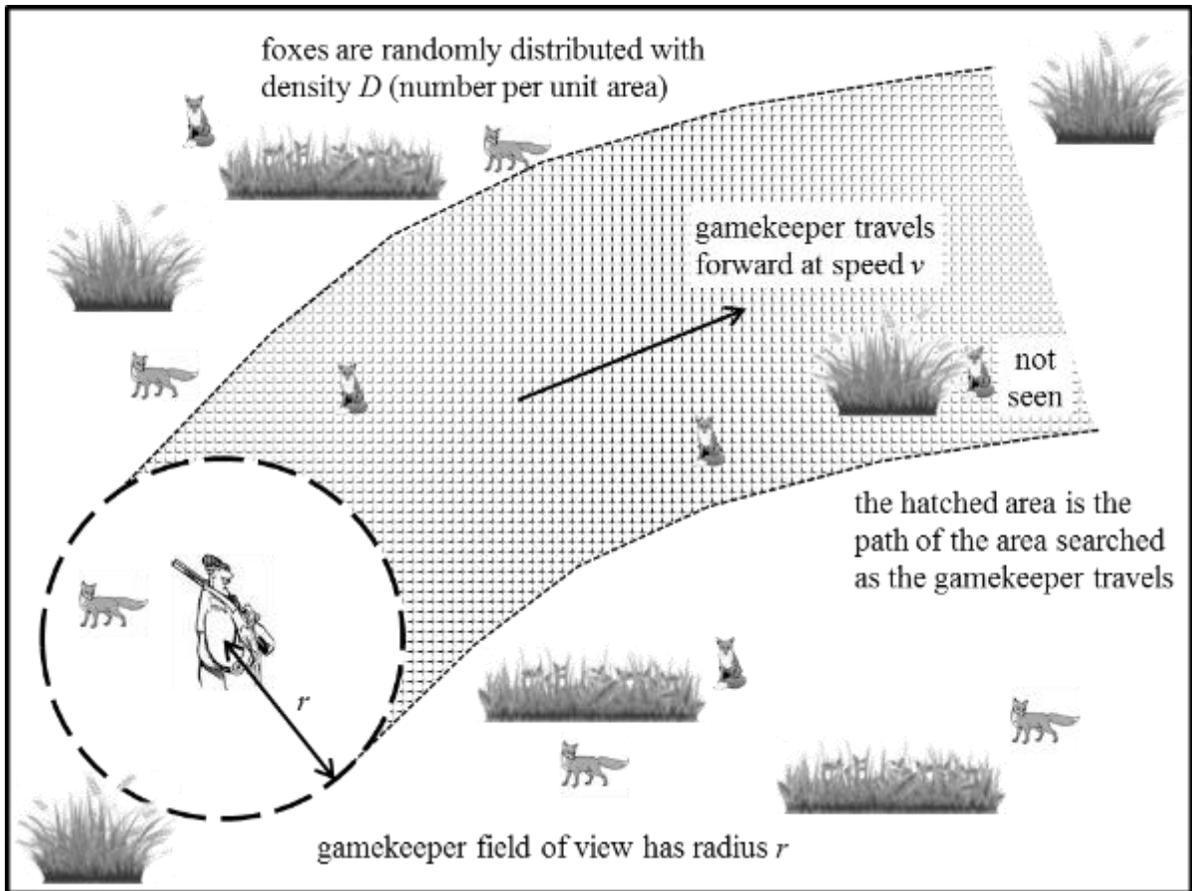


Figure 6.2. A gamekeeper searching for foxes across an estate. The area searched is determined by the gamekeeper's velocity and their field of view, with the fraction of the population seen within this area determined by the sighting probability (adapted from Case 2000).

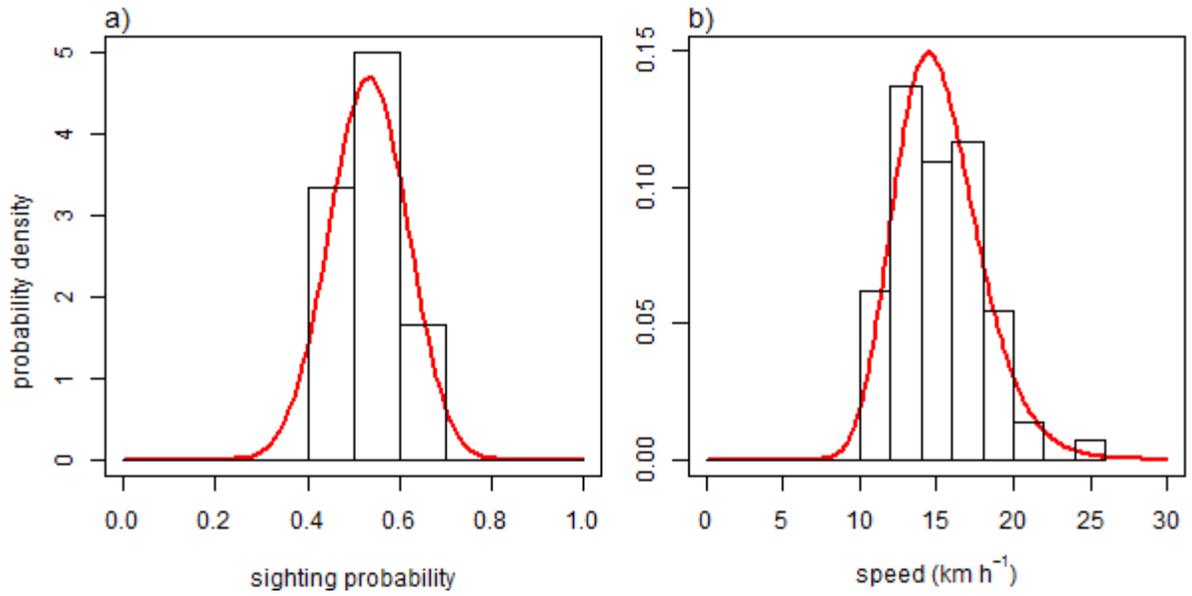


Figure 6.3. Estimated values (histogram) and best fit probability distribution (red line) of a) sighting probability ($n = 6$ estimates) and b) speed of travel ($n = 69$) from reanalysis of the distance sampling data from Heydon *et al.* (2000).

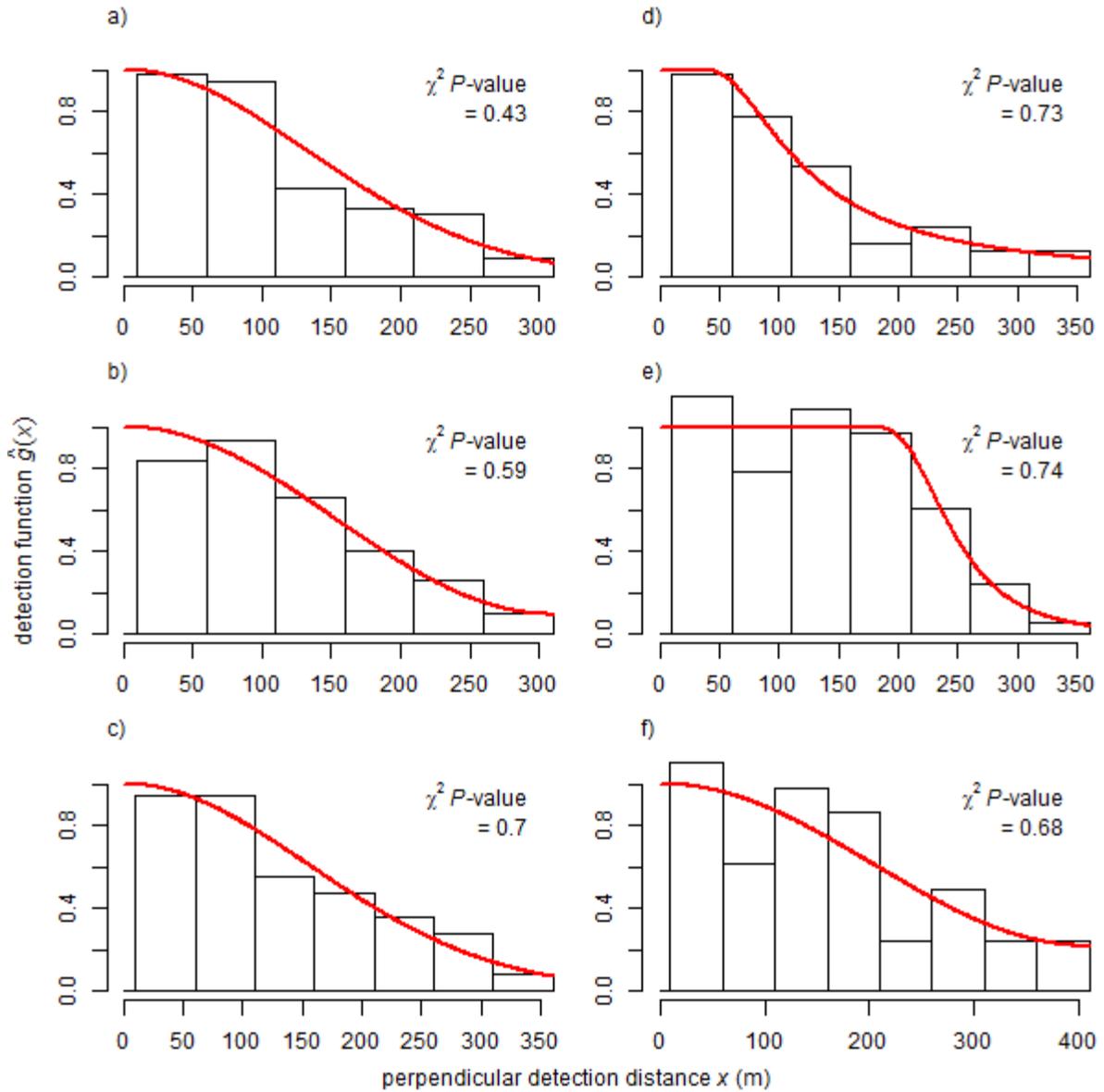


Figure 6.4. Histograms of grouped distance data with fitted detection functions fits to distance sampling data, showing χ^2 goodness-of-fit P -value. a) Wales – autumn survey ($n = 101$ fox sightings); b) Midlands – autumn ($n = 232$); c) East Anglia – autumn ($n = 92$); d) Wales – spring ($n = 72$); e) Midlands – spring ($n = 81$); f) East Anglia – spring ($n = 39$).

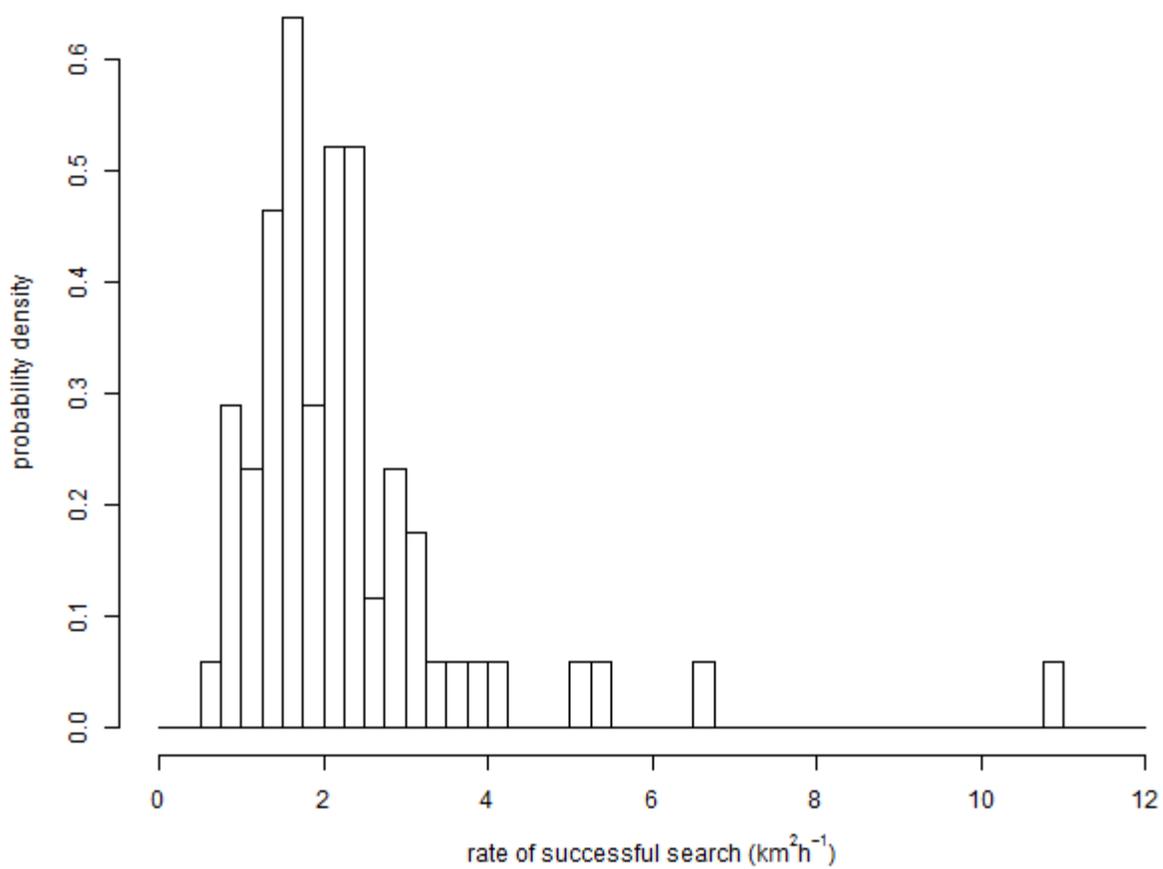


Figure 6.5. Histogram of empirical rate of successful search estimates ($n = 69$) obtained from distance sampling analysis.

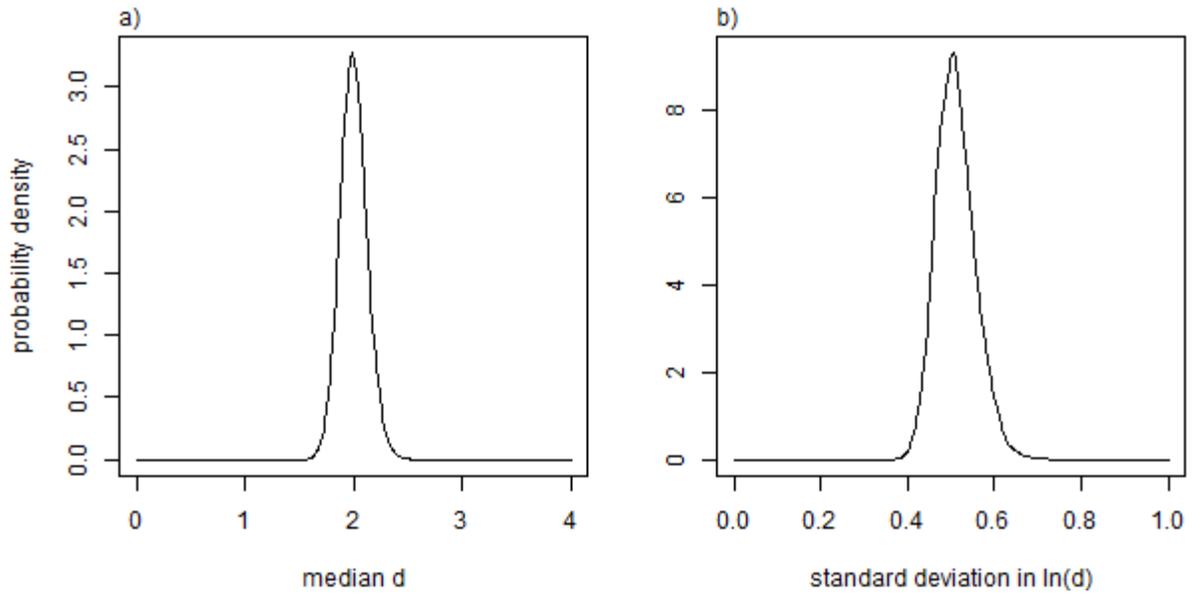


Figure 6.6. Posterior probability density functions for a) the median rate of successful search and b) the standard deviation in the natural logarithm of the rate of successful search estimates.

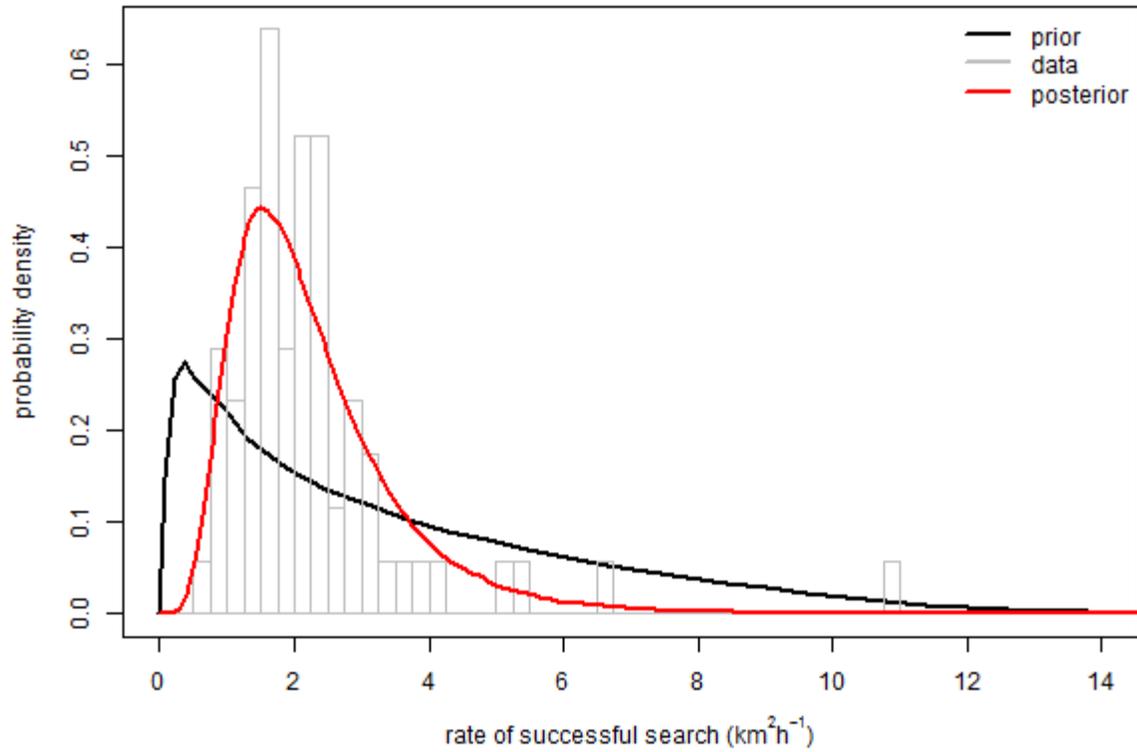


Figure 6.7. Posterior predictive distribution for the rate of successful search, the empirical rate of successful search data obtained from distance sampling, and the least informative conceptual prior.

Chapter 7: Population dynamics of foxes during restricted-area culling in Britain

7.1 Introduction

To reduce predation on ground-nesting birds, red fox (*Vulpes vulpes*) populations in rural Britain are controlled by culling on restricted areas such as game-shooting estates and wildlife reserves. Lethal control of predators is a controversial practice and it is increasingly necessary to evaluate the benefits of killing animals against the welfare costs (Fall & Jackson 2002). A key part of this evaluation is to demonstrate the effectiveness of culling in reducing local fox density (Baker & Harris 2006). Provided that there are suitable abundance index data on the fox population within the culled area, this can be achieved using population dynamics modelling.

Simulation models are capable of providing useful insights if suitable parameter values are available. Previous authors modelling fox populations on restricted areas concluded that immigration is an important factor in the dynamics of culled populations (Harding, Doak & Albertson 2001; McLeod & Saunders 2014). These studies were simulation-based and used parameter values from the literature to reconstruct populations with fox density similar to a previously observed density or relative measure of abundance. Using these models it was therefore possible to infer the level of control which must have occurred to best explain the known removals. However, for parameters such as immigration rate and carrying capacity there is very little information. There is also large variation in fox density and demographic parameters at both local, landscape and regional scales due to variation in factors such as food availability and fox culling pressure (Heydon & Reynolds 2000b; Heydon, Reynolds & Short 2000; Baker & Harris 2008; Devenish-Nelson *et al.* 2013). Obtaining reliable inferences using a simulation-based modelling approach therefore requires estimates of parameters to be available from the literature and also be representative of the local population.

For the dynamics of local fox populations to be reliably understood in relation to culling effort on a restricted area, the parameters determining the key population processes must be estimated from data relevant to that area. Fitting the open-population depletion model developed in Chapter 3 within a Bayesian state-space modelling framework makes it possible to estimate immigration, cub recruitment and non-culling mortality at the estate scale using data on culling effort and success obtainable from gamekeepers. Given reconstructions of the within-year fox density using this model the effectiveness of fox control on different estates across Britain can be determined.

State-space models are a special type of hierarchical model that can estimate deterministic parameters, process error and observation error simultaneously (Buckland *et al.* 2007; Bolker 2008; Lebreton & Gimenez 2013). State-space models make it possible to estimate complex population processes in the presence of measurement error and therefore to obtain more reliable inferences. Nevertheless, state-space models are data-hungry and insufficient information in the data can lead to model parameter identifiability problems (Schnute 1994; Bolker 2008; Trenkel 2008). Datasets of the type available from gamekeepers on culling effort and success are fortunately large. Data in the FMS were recorded on a daily time-step, and despite aggregating these data into longer weekly (or two-weekly) time-steps the number of time-steps was >100 for most estates. The simulation-estimation study in Chapter 3 indicated that time series spanning three or more fox breeding periods and which did not have long periods of missing data resulted in reliable parameter and fox density estimates, especially when informative priors were used.

However, the simulation-estimation study results did reveal some identifiability issues with the model, in particular that the standard deviation in lognormal process errors σ_p was only weakly identifiable. Although the estimates of fox density were minimally biased and the bias in estimates of σ_p was not large (median PRB <10%), the estimates from some simulated datasets had 80% credible intervals that did not contain the true value. This problem increased as the time series of data became shorter. Problems estimating σ_p were perhaps unsurprising as “estimation of both process and observation uncertainties is one of the great challenges in state-space modelling” (Thorson, Ono & Munch 2014). Some

method was therefore required to overcome this weak identifiability problem and avoid damaging the reliability of other parameter estimates, such as carrying capacity. The options included: 1) following the approach used for other parameters and specifying an appropriate informative prior, or 2) fixing σ_p at some value and performing sensitivity analysis. Both options require some knowledge of the variability in fox populations due to process error. This information was lacking as this thesis is the first known application of state-space modelling to fox populations. The option of specifying an informative prior was not possible and so a suitable value at which to fix σ_p at was needed.

Ecological applications of state-space models are still growing in number, but most of the earliest applications were in fisheries (e.g. Schnute 1994; Meyer & Millar 1999b). In fisheries, a value of 0.05 for σ_p is considered low and a value of 0.20 for σ_p is considered high for annual time steps (Thorson, Ono & Munch 2014). So far there are only a handful of state-space modelling applications to terrestrial systems and the estimates of σ_p from these studies are summarised in Table 7.1. From these it appears that σ_p estimates larger than 0.20 are seemingly not uncommon in populations of mammal and bird species (e.g. Knappe, Jonzén & Sköld 2011; Hosack, Peters & Hayes 2012; Iijima, Nagaïke & Honda 2013). Intuitively, terrestrial systems are subject to higher levels of process variability compared to marine systems because the environment is less stable and human actions cause additional variability. Given these considerations, σ_p for foxes was fixed at 0.2 (for a two-weekly time step) and evaluations of the sensitivity of results to both lower and higher values conducted.

State-space models used in both fisheries and terrestrial applications have typically estimated process errors on annual time-steps because the models used were modelling recruitment-only and not immigration. Because of the multiplicative nature of lognormal process error, weekly or two-weekly values of σ_p must be smaller than for annual time-step models. But modelling immigration as well as recruitment potentially increases the process variation. This model for foxes on restricted areas assumes a mean immigration rate which, though variable, is not related to season. In reality, the number of foxes moving onto or off the culling area may vary substantially around this mean rate from one time-step to the next. At the upper extreme, during the post-weaning period, a vixen (or more than one) may move

with a family group onto or off an estate. Movements of vixens with cubs of up to 1.5 km are not uncommon (Lloyd 1980; Reynolds, Goddard & Brockless 1993). This degree of variation would not be allowed if σ_p was fixed at too small a value. A further reason to expect higher process variation in restricted-area fox populations is the population size. Given a density of 2 fox km⁻² and an estate of 5 km², the number of foxes is small enough that loss or gain of a single fox results in a large (10%) proportional change in density.

Local similarity in parameter estimates from estates was anticipated given similar habitat features and fox culling pressure within landscapes or regions. This suggested the potential for improved estimation using spatial Bayesian hierarchical models (e.g. Su, Peterman & Haeseker 2004). However, similarities in model parameters within regions or landscapes may be less than expected because of factors which cause local variation. For instance, in Chapter 4 an analysis of immigration rates found that released gamebird density explained some of the variation in immigration rate at the landscape scale. Although there are large-scale (regional and landscape) patterns in gamebird release densities (Chapter 4, see also Tapper 1992), management decisions about releasing are taken on individual estates and the variation in release density among estates within a region or landscape can be very large (Chapter 4). If gamebird releasing is a factor in fox population dynamics, this could lead to significant local variation in parameter estimates. It was therefore of interest to examine relationships between demographic parameter estimates and gamebird release density where data were available.

This Chapter aimed to use the open-population depletion model developed in Chapter 3 to estimate demographic parameters and reconstruct fox density using a Bayesian state-space modelling framework, characterize seasonal patterns of variation in fox density, and evaluate the relationship between lamping effort and fox density on estates throughout Britain. This was to be achieved initially using a non-hierarchical model, following which a spatial hierarchical model would be considered. The sensitivity of parameter estimates to structural assumptions, specifications of prior distributions, process error variation and observation error distribution was then examined.

7.2 Methods

7.2.1 Data

Only 22 of the 75 estates that contributed to the Fox Monitoring Scheme (FMS, Chapter 2) met the criteria for required data (Table 7.2). Because FMS data were contributed confidentially, estate names are presented here using randomly-assigned three letter codes to preserve anonymity. The area of individual estates ranged from 1.6 to 36.4 km². Gamekeepers contributing to the FMS were self-selected as keen users of lamping and this method accounted for the majority of foxes killed on FMS estates (Chapter 2). A reasonable representation of fox culling pressure is therefore annual lamping effort per km². This varied considerably between estates and years (Table 7.2). On average, across estates the amount of lamping effort deployed decreased over time.

The majority of estates ($n = 16$) were located in eastern England. Precise locations of the FMS estates were not available as estate boundary information was not contributed. Instead, the gamekeepers postal address was contributed, and for most estates a grid reference. These two sources of information did not consistently provide evidence for precise estate location and the most likely location had to be inferred using a map. For estates close to landscape type boundaries this created uncertainty over the landscape type which covered the largest proportion on each estate. It was thus only possible to state that all eastern England estates were most likely located within the arable b landscape type. There were also estates in southwest England, most likely within the pastural a ($n = 3$) and arable a ($n = 2$) landscape types. One estate was located in Scotland, most likely in the upland landscape.

Culling effort and success data (lamping effort E_t , fox sightings Y_t , lamping cull L_t , other method cull S_t , cub at earth cull C_t) from each estate were initially aggregated into weekly time-steps. However, the computation time of initial model runs using these data was deemed too long (up to 24 hours per estate), so the data were further aggregated into a two-weekly time-step so that analyses were tractable. This also required that the weaned cub distribution, w_t , defined in Chapter 3 was aggregated into a two-weekly time-step. Estimates

of parameters and fox density from these initial runs were found to be within 5% of those obtained using two-weekly time-steps, so all analyses used data on the two-weekly time-step.

7.2.2 Bayesian state-space model

The state-space open-population depletion model and the assumptions made by it are fully described in Chapter 3 and so it is not fully described here. However, the estimation model equations are re-introduced. The fox population on each estate was modelled in units of density so that parameter estimates would be comparable across estates. To reduce correlation between the fox density latent states N_t and carrying capacity K , and thereby improve the slow mixing of the Markov chains, the model was re-parameterised by expressing fox density as a proportion of carrying capacity ($P_t = N_t/K$; Meyer & Millar 1999a; Millar & Meyer 2000b). P_t in two-weekly time-step t was assumed to follow the state equations:

$$P_1 = (N_0/K)e^{\varepsilon_1} \quad \text{Eq. 7.1}$$

$$P_t = \{P_{t-1}e^{-M} + [v/K(1 - P_{t-1})] + G_{t-1} - (L_{t-1}/K) - (S_{t-1}/K)\}e^{\varepsilon t} \quad \text{Eq. 7.2}$$

$$G_t = w_t r P_t (1 - P_t) - (C_t/K) \quad \text{Eq. 7.3}$$

where G_t represents weaned cubs recruiting in time-step t , L_t is the cull from lamping, S_t is the cull from snaring/other methods, and C_t is the cull of cubs at earths, which are assumed to be pre-weaned cubs. All observed (i.e. recorded) cull numbers were converted to density of foxes killed per km² using the estate area, A . To account for cubs being killed at earths in any week from birth until weaning age, rather than just in the week they recruit as implied in Eq. 7.2, all cubs culled at earths in year y were summed and re-distributed into each recruitment week t following the w_t schedule to calculate normalised values for C_t within each year:

$$C_{t,y} = w_t \sum_{y=1996}^{2000} C_{t,y}^{obs} \quad \text{Eq. 7.4}$$

This was necessary to ensure that cubs culled at earths within each year were not removed from the model before they had been produced in a given week t . For numerical stability, P_t was constrained within the model to be non-negative (≥ 0.0001). Process errors were assumed to be independent and identically distributed (iid) multiplicative lognormal (Halley & Inchausti 2002), where ε_t were randomly sampled from standard normal distribution that has a standard deviation σ_p :

$$\varepsilon_t \sim \text{Normal}(0, \sigma_p) \quad \text{Eq. 7.5}$$

Initial model runs on some estates estimated σ_p using a vague prior and resulted in very large posterior medians for σ_p (>0.5). This confirmed the need to fix σ_p . The estimate of $\sigma_p=0.08$ from a model of the Scandinavian wolf population (Liberg *et al.* 2012) seemed taxonomically relevant, except that these authors were modelling recruitment only on an annual time-step and the wolf population considered was >200 individuals. Higher process variation was expected in the fox populations and so the decision was made to fix σ_p at 0.2 at a two-weekly time step and to examine the consequences of this choice through sensitivity analysis.

The model was fitted to the observed number of fox sightings, Y_t , with the observation errors assumed to be Poisson distributed:

$$\hat{Y}_t = dE_tP_tK \quad \text{Eq. 7.6}$$

$$Y_t \sim \text{Poisson}(\hat{Y}_t) \quad \text{Eq. 7.7}$$

where d is the rate of successful search in units $\text{km}^2 \text{hr}^{-1}$ and E_t is the number of lamping hours in t . For presentation of fox density, the marginal posterior estimates of N_t were obtained as the product of P_t and K .

7.2.3 Prior probability distributions for parameters

The estimated parameters in the model were N_0 , K , v , r , M , and d . Informative priors for v , r , M , and d were used based upon the analyses in Chapters 4-6 and Appendix D (Table

7.3). The posterior predictive distribution for all landscape types from the immigration rate meta-analysis (Chapter 4) was chosen as the prior for ν . This was because the CV of most landscape specific predictive distributions was <0.2 , which is too precise for use as a prior. Instead, the posterior predictive distribution provided a prior that included the key information from the analysis but because it was less precise it was less likely to exclude the true value of ν on an estate should it be considerably different from the previously obtained central tendency for that landscape type. This also accounted for the uncertainty about the landscape type each estate was located in.

For use with data on a two-weekly time-step, ν and M were changed from annual rates to two-weekly rates. For easier interpretation, these two parameters are presented in the results as weekly rates. Vague priors were set for N_0 and K and took the same uniform distribution with the upper bound equal to the fox density in an urban population from Bristol (13.9 fox km^{-2} , Soulsbury *et al.* 2007). The Bristol population was at this density for several years prior to a period when the density tripled and an epizootic of mange occurred, so it was considered to be a ‘healthy’ urban density representing the maximum a rural population might reach if food and den site availability in rural areas was increased to urban levels, and there were no sympatric carnivores, i.e. badgers, that could affect fox density (Trewby *et al.* 2008). As there was no knowledge of the culling history on each estate, N_0 was assumed able to be any value within the bounds of K but not higher.

7.2.4 MCMC simulations

Samples from the joint posterior probability distribution of the unknown parameters and latent states $p(N_0, K, \nu, r, M, d, N_t \mid \text{data})$ were simulated by MCMC integration using WinBUGS 1.4 (Spiegelhalter *et al.* 2007) implemented from within the R statistical software (R Core Team 2013) using the R2WinBUGS package (Sturtz, Ligges & Gelman 2005). The posterior was estimated from two independent MCMC chains with initial values chosen randomly from the joint prior. In the Markov chains, some parameters showed strong autocorrelation. To reduce the problem only 1 in 100 iterations were recorded after the first 100,000 iterations were removed as the burn-in. Inferences were then derived from a sample

of 20,000 iterations from two chains of 10,000 iterations. Convergence of the Markov chains to the posterior distribution was diagnosed using the R coda package (Plummer *et al.* 2006). Gelman-Rubin convergence statistics (Gelman *et al.* 2004) were <1.1 for all parameters and Geweke's Z-scores (Geweke 1992) did not fall within the extreme tails of a standard normal distribution, suggesting that the chains had fully converged. Initial runs were slow and took up to 24 hours computation time, so in addition to aggregating data onto a two-weekly time-step, parallel computing was used to increase estimation speed using the R snowfall package (Knaus 2013). Depending upon the length of the sighting rate time series, final runs therefore took 3-6 hours per estate.

Post-model-pre-data probability distributions are a diagnostic showing how the priors interact with a model given the removal data but before the model is fitted to an abundance index (McAllister 2014). Estimating post-model-pre-data distributions does not involve updating of the priors as sampling is performed directly from the joint prior probability distribution. This allows for an evaluation of the extent to which fitting the model to sighting data updates the distributions determined by the interaction of the priors and inputted culling data within the model formulation. The post-model-pre-data distribution for fox density in the final time-step was estimated and later compared to the posterior for fox density in the final time-step to show the extent of posterior updating on each estate.

7.2.5 Culling vs. non-culling mortality

The relative contribution to the mortality from culling (T_t) and from non-culling factors (X_t) was assessed by using the estimates of fox density and non-culling mortality rate to calculate non-culling mortality in time-step t as:

$$X_t = N_t - N_t e^{-M} \quad \text{Eq. 7.8}$$

where N_t is the posterior median fox density and M is the posterior median for instantaneous non-culling mortality rate on a two-weekly time-step. Culling mortality was calculated as:

$$T_t = (L_t + S_t)/A \quad \text{Eq. 7.9}$$

The cumulative mortality from both culling and non-culling mortality was calculated on each estate and examined relative to estimated fox density and carrying capacity.

7.2.6 Sensitivity analysis

The sensitivity of the model parameter and fox density estimates to four types of assumption was examined as follows.

7.2.6.1 Structural assumptions

In the estimation model, immigration was assumed to be a year-round constant process but an alternative assumption could be that it is a seasonal process based upon the August to March dispersal period. This assumption was examined by running a version of the model where immigration did not occur during April-July. It was achieved by populating a one-year long binary vector, i.e. 26 time-steps, with a zero if the time-step was in April-July and a one if the time-step was in August-March. The sum of this vector was calculated in order to scale the ones and ensure the sum totalled 26. This was necessary to maintain the same annual immigration rate under either assumption for comparison. The vector was then used to multiply v in Eq. 7.2 in each time-step. The results from the reference model assuming constant immigration was then compared to those from the model assuming seasonal immigration. The timing of cub recruitment was also examined. This was achieved by moving the weaned cub distribution two weeks (one time-step) earlier or two weeks later to account for cubs being born earlier or later on average across the estate.

7.2.6.2 Prior probability distribution specification

The value used for the upper bound of the vague uniform prior for K of 13.9 fox/km² (Table 7.3) was the spring density in an urban population from Bristol during a relatively stable pre-mange period (Soulsbury *et al.* 2007). This population reached a higher density of 25.8 fox km⁻² in the spring preceding a mange epizootic, and then 37.0 fox km⁻² in the first year of the ensuing epizootic period. Therefore, the sensitivity to a higher upper bound for K of 25.8 fox km⁻² was examined as in theory a rural population could reach such a high density if there was enough food available. The informative lognormal prior chosen for M

was based upon the Hoenig method (Chapter 5). This was chosen in favour of the alternative lognormal prior based upon the McCarthy method, in which the prior median was $\ln(0.274/26)$ with a CV of 0.60. Sensitivity of the results to use of this prior was also examined. The sensitivity to the informative prior for r developed in Appendix D was also examined by using a vague uniform prior with a lower bound at zero and an upper bound at $6.0 \text{ cub fox}^{-1} \text{ yr}^{-1}$.

7.2.6.3 Process error specification

The decision to fix σ_p at 0.2 was examined by 1) use of alternative fixed values 0.05 and 0.1; 2) use of priors that made σ_p estimable; and 3) calculation of empirical σ_p . Two priors were assessed 1) a vague uniform prior with a lower bound at 0.001 and an upper bound at 1.0, and 2) an informative lognormal prior with a median equal to $\ln(0.05)$ and a CV equal to 0.2 to give high certainty around a small value for σ_p . Empirical σ_p provides an indication of whether the realised process errors ε_t from the estimation are smaller or larger on average than assumed in the model. The empirical estimates of σ_p are dependent upon the structural assumption for the observation errors. In BUGS code it was possible to extract the vector of ε_t that is the length of the time series for each MCMC iteration as the difference between the deterministic parts of Eq. 7.1 and Eq. 7.2 that are not subject to lognormal process error, i.e. those parts between parentheses/brackets, and the simulated value of P_t that is subject to process error. Empirical σ_p is then calculated as the standard deviation in ε_t . These values can then be summarised for each estate by taking the mean over the number of iterations.

7.2.6.4 Observation error specification

Incorrect specification of the observation model can markedly affect inference using state-space models (Knape, Jonzén & Sköld 2011). A potential issue in this regard was the occurrence on many estates of weeks without any lamping effort and therefore without sighting data. This could conceivably cause (over-)dispersion not accounted for by the Poisson distribution. Sensitivity of results to alternative observation error distributions was therefore examined. The negative binomial distribution with mean parameter μ and

dispersion parameter φ was considered for the observation model. This is the ecological parameterisation, also known as the Pólya distribution, where the dispersion parameter φ is a non-negative continuous number. In the parameterisation available in BUGS, known as the Pascal distribution, the parameter related to φ is discrete. This made use of the negative binomial distribution challenging, as it was necessary to use a Poisson-Gamma mixture distribution to suitably model the sighting data (McCarthy 2007; Wenger & Freeman 2008). Assuming that μ is equal to \hat{Y}_t as calculated in Eq. 7.6, under this approach if:

$$Y_t \sim \text{Poisson}(\rho\mu) \quad \text{Eq. 7.10}$$

where:

$$\rho \sim \text{gamma}(\varphi, \varphi) \quad \text{Eq. 7.11}$$

then:

$$Y_t \sim \text{NegBinomial}(\mu, \varphi) \quad \text{Eq. 7.12}$$

Two types of negative binomial observation model were examined. The first model had a fixed value for φ that was obtained from the sighting data before running the estimation model. This was achieved by recognising that the variance of a negative binomial random variable may be calculated using the formula:

$$\hat{\sigma}_Y^2 = \mu_Y + \mu_Y^2 / \varphi \quad \text{Eq. 7.13}$$

where μ_Y is the observed mean Y_t and $\hat{\sigma}_Y^2$ is the estimated variance in Y_t given φ . The observed variance in sightings σ_Y^2 was calculated, allowing least-squares to be used to minimise the difference between $\hat{\sigma}_Y^2$ and σ_Y^2 and obtain the maximum likelihood value for φ . This was performed in the R statistical software (R Core Team 2013). The second model used a vague uniform prior on φ with lower and upper bounds of 0.001 and 25, respectively.

The lognormal distribution was also considered for the observation model, where continuous sighting rate was modelled rather than discrete sightings. Under this approach

$$Y_t \sim \text{lognormal}(\ln(\hat{Y}_t), \sigma_{obs}) \quad \text{Eq. 7.14}$$

where σ_{obs} is the standard deviation in lognormal observation errors. σ_{obs} was estimated using a vague uniform prior with lower and upper bounds of zero and one, respectively.

7.2.7 Relationships with gamebird release density

The potential influence of gamebird release density on parameter estimates was examined on those estates for which release data were available. The National Gamebag Census database was queried for shooting estates which submitted gamebird bag and release records annually during 1996-2000 and which were also contributors to the FMS (extracted on 7 October 2013). Data were summarised for each estate by calculating the mean annual bag density of shot birds and the mean annual release density. The mean annual density of birds not shot was also calculated, from the difference between the density of birds released and the density of birds shot. The posterior median estimates for model parameters were then examined in relation to these data using linear regression.

7.3 Results

7.3.1 Parameter estimation

Sighting and effort data were modelled on a two-weekly time-step to estimate parameters for 22 estates. The priors for most model parameters were updated considerably on all estates (Figure 7.1). The post-model-pre-data distributions for N_t in the final weeks were also updated on all estates. The marginal posterior updates are most obvious for those parameters which had vague priors, N_0 and K . Posterior medians for N_0 ranged between 0.24 and 5.69 fox km⁻², with most estates being below 3.5 fox km⁻² (Table 7.4). CV for N_0 was generally larger than 0.5, with the estimates with larger CV characterised by the sighting rate time series on these estates being more variable during the first few weeks of data. Posterior medians for K ranged between 1.98 to 8.47 fox km⁻².

Parameters with informative priors were also updated, particularly v and d . Posterior medians for v ranged between 0.024 and 0.561 fox km⁻² wk⁻¹. Most of the updates were an

increase relative to the prior median of $0.046 \text{ fox km}^{-2} \text{ wk}^{-1}$. The highest estimate for ν was from YEM which had the largest culling pressure and annual bag density. Posterior medians for d ranged from 0.19 to $0.86 \text{ km}^2 \text{ hr}^{-1}$, which meant on all estates that the updates were a decrease relative to the prior median of $2.00 \text{ km}^2 \text{ hr}^{-1}$. Posterior medians for r ranged between 1.16 and $3.63 \text{ cub fox}^{-1} \text{ yr}^{-1}$. The amount of updating was variable and for many estates the posterior median was similar to the prior median of $3.06 \text{ cub fox}^{-1} \text{ yr}^{-1}$, with the posterior precision being only a small improvement on the prior precision ($\text{CV} = 0.35$). M was the parameter with least updates to the prior median of 0.0090 wk^{-1} , as the posterior medians ranged between 0.0070 and 0.0106 wk^{-1} . The precision was usually not an improvement on the prior precision ($\text{CV} = 0.56$).

Across all estates, posterior correlations between any of the parameters were not strong as correlation coefficients were all lower than 0.7 . There were moderate posterior correlations (0.4 - 0.7) between N_0 and d (negative) on $17/22$ estates and between K and d (negative) on $11/22$ estates. Correlation coefficients between all other parameters reflected weak posterior correlation. There was considerable spatial variation in parameter values across estates (Figure 7.2) and use of a spatial hierarchical model was not pursued. The only parameter for which there was a suggestion of spatial clustering was M as all the highest values were in the east, but there was no conclusive east-west pattern. For all other parameters, estates relatively close to each other had highly variable values, particularly for K and ν . The post-model-pre-data distributions for N_t in the final weeks were also updated on all estates (Figure 7.3–Figure 7.8, Appendix E).

7.3.2 Density reconstruction

The model fitted the observed sighting rate time series well on all estates. There were large differences between estates in the range of sighting rates, with a maximum sighting rate of $0.81 \text{ fox seen hr}^{-1}$ on HIR (Figure 7.5a) compared to $5.14 \text{ fox seen hr}^{-1}$ on NYP (Figure 7.7a). Estimates of pre-breeding fox density, determined as the mean of the posterior median for N_t in February and March, ranged from 0.89 to 3.81 fox km^{-2} . Pre-breeding fox density

as a proportion of median carrying capacity ranged from 20% to 83%, indicating that the fox population was suppressed on all estates to varying degrees.

Results from six estates (CUL, DLQ, HIR, NOG, NYP and VAR) were chosen as case studies and are interpreted in more detail given the lamping effort and number of foxes killed (Figure 7.3–Figure 7.8). Results from the 16 other estates to which models were fitted can be found in Appendix E. The mean fox density on CUL was 2.15 fox km⁻² (Figure 7.3b). The level of culling effort was relatively low (Table 7.2) but there was a constant removal of foxes during the year with a mean weekly cull of 0.062 fox km⁻² wk⁻¹. Pre-breeding N_t was suppressed by 59% relative to K (Figure 7.3c). The mean annual cull was greater than the mean fox density, but although the fox density was suppressed relative to what would be expected in the absence of culling, this level of culling pressure was not enough to maintain a low fox population during the bird nesting period. The posterior medians for CUL were average relative to the posterior medians estimated on the other estates (Figure 7.3d, Table 7.4).

The mean fox density on DLQ was 3.27 fox km⁻² (Figure 7.4b). The annual level of lamping effort on this estate was average (Table 7.2) but was concentrated into the period just before and during the bird nesting period. The mean weekly cull was 0.166 fox km⁻² wk⁻¹ and the high culling pressure on DLQ led to generally high suppression of fox density, especially during the nesting period when culling was targeted. Pre-breeding N_t was 53% of K and N_t was less than 50% of K for considerable periods of time. For short periods N_t was close to zero (Figure 7.4c). The posterior median for immigration rate onto DLQ was among the highest values relative to other estates, as were the values for carrying capacity and initial density, while rate of successful search was one of the lower values estimated (Figure 7.4d, Table 7.4).

The culling effort on HIR was spread throughout the year but the level of lamping effort was the highest (Table 7.2). The mean weekly cull was high at 0.110 fox km⁻² wk⁻¹. The mean fox density on this estate was 0.92 fox km⁻² and the sighting rates were low (Figure 7.5a,b). The population was highly suppressed relative to K with pre-breeding N_t 32% of K (Figure 7.5c). The posterior median for carrying capacity was low relative to other

estates, but the values for the other parameters were close to average (Figure 7.5d, Table 7.4).

The mean fox density on NOG was 2.38 fox km⁻² (Figure 7.6b). Culling effort was applied year-round and lamping effort was of average intensity (Table 7.2). The mean weekly cull was 0.084 fox km⁻² wk⁻¹, though notably no cubs were killed at earths in any year. The fox population was well-suppressed during the winter and early part of the bird nesting period prior to cub recruitment, but because there was no control of cubs the population increased sharply at this time (Figure 7.6c). Pre-breeding N_t was 40% of K . The posterior medians for NOG were average relative to the posterior medians estimated on the other estates (Figure 7.6d, Table 7.4).

The mean fox density on NYP was 3.72 fox km⁻² and the sighting rates were up to twice those seen on other estates (Figure 7.7a,b). Culling effort was applied throughout most of the year but at a relatively low level (Table 7.2). The mean weekly cull was 0.080 fox km⁻² wk⁻¹. Suppression of the fox population was poor, and during one winter N_t spent a large number of weeks above K (Figure 7.7c). Pre-breeding N_t was 83% of K . The posterior median for immigration rate onto NYP was high relative to the posterior medians estimated on the other estates (Figure 7.7d, Table 7.4).

Sighting rates on VAR were low and the reconstructed mean fox density was 1.05 fox km⁻² (Figure 7.8a,b). Culling effort was applied year-round. Lamping effort averaged almost 540 hours per year, the highest value for any of the 22 estates, although this was not a particularly high lamping effort relative to estate area (Table 7.2). The mean weekly cull of 0.035 fox km⁻² wk⁻¹ was low compared to HIR where fox density was similar, but the suppression of N_t relative to K was very high, in particular from 1997 onwards (Figure 7.8c). Pre-breeding N_t was 29% of K . The posterior median for immigration rate was low relative to other estates and *per capita* birth rate was the lowest estimate (Figure 7.8d, Table 7.4).

7.3.3 Mortality comparison

The contribution of non-culling mortality to total mortality was small relative to the culling mortality on all estates (Figure 7.9). On over half of the estates the annual culling mortality exceeded the carrying capacity. Annual non-culling mortality was on average around 20% of carrying capacity. Cumulative non-culling mortality typically exceeded carrying capacity after about two years, suggesting population turnover in two years in the absence of culling.

7.3.4 Sensitivity analyses

Sensitivity of the parameter and fox density estimates to structural and prior assumptions was assessed on the six estates used as case studies (CUL, DLQ, HIR, NOG, NYP and VAR). Parameter estimates were robust to the structural assumptions related to timing of weaned cub recruitment (Figure 7.10) and there was no effect on N_t (Figure 7.11a). The assumption that immigration was a seasonal process resulted in differences in some parameter estimates compared to the constant immigration reference case, in particular v , K and d on HIR, NYP and VAR (Figure 7.10). The effect of the seasonal immigration assumption did not affect fox density on 3/6 estates as N_t was almost identical compared to the reference case on CUL, NOG and DLQ (Figure 7.11a). However, the seasonal immigration assumption did result in lower N_t estimates on NYP and VAR and higher N_t estimates on HIR, though the difference in N_t never exceeded one fox per km². There was no effect from using a higher upper bound on the uniform prior for K compared to the reference case. There was an effect of using the informative prior on r but this was restricted to the marginal posterior for r (Figure 7.10) and not to N_t , which was almost identical to the reference case (Figure 7.11b). There was an effect of using the McCarthy informative prior for M instead of the Hoenig informative prior, but this was also restricted to the marginal posterior for M (Figure 7.10) and not to N_t (Figure 7.11b).

The mean estimates of empirical process error standard deviation were all lower than 0.2 (assuming Poisson observation errors), with the mean across estates equal to 0.12 (Figure 7.12). This indicated that the realised process errors were smaller on average than assumed

in the model. Estimates of empirical σ_p were similar assuming negative binomial observation errors, being 0.01 lower on those estates assessed. Sensitivity of the parameter and fox density estimates to process error and observation error assumptions was assessed on DLQ and VAR only. These analyses showed that parameter and N_t estimates were sensitive to values of σ_p that were smaller than the 0.2 used in the reference case. Using fixed values for σ_p of 0.05 and 0.1, mean fox density on DLQ was estimated to be higher by 68% and 44%, respectively (Figure 7.13); and on VAR by 104% and 51%, respectively (Figure 7.14). The maximum difference in density estimates was up to 4.91 fox km⁻² on DLQ and 2.49 fox km⁻² on VAR. The higher N_t estimates corresponded with lower estimates of the rate of successful search. On DLQ, the use of either a vague or informative prior for σ_p did not have as large an effect on parameter or N_t estimates (Figure 7.13). This was despite large differences in the marginal posteriors for σ_p . The posterior median using an informative prior was close to 0.05, but using a vague prior it was 0.30.

On VAR, the use of an informative prior for σ_p had little effect on parameter or N_t estimates as the posterior median of 0.16 was close to the reference case where σ_p equalled 0.2 (Figure 7.14). However, use of a vague prior resulted in a posterior median for σ_p of 0.52, a considerably higher value and the highest among all estates. This resulted in a much lower value for K , with effects also found on v , r and d . N_t was estimated to be up to 50% lower when using a vague prior for σ_p , and N_0 was estimated to be almost four times K which on an estate under this level of culling effort seemed highly unlikely. The process error sensitivity analyses were subject to convergence problems for some parameters, particularly on DLQ when σ_p was fixed at 0.05 and when the informative prior was used (Figure 7.13).

The results were not sensitive to the choice of likelihood function to model the observed sighting data when σ_p was fixed at 0.2, except on VAR in the case where sightings were assumed to be from a negative binomial distribution with a fixed dispersion parameter (Figure F.1, Figure F.2). In this case the model encountered convergence problems for v and estimated lower values for K and N_t . When a vague prior was used to estimate σ_p on DLQ, the estimates for both parameters and N_t were similar under all likelihood function choices (Figure F.3). On DLQ, the posterior median of 0.30 for σ_p was not much larger than the

reference case of 0.2, a difference which when Poisson observation errors were assumed had caused minimal effects (Figure 7.13). However, use of a vague prior to estimate σ_p on VAR had resulted in large effects under Poisson observation errors (Figure 7.14), and when alternative observation errors were assumed this caused some large effects in parameter estimates relative to Poisson observation errors, though these were restricted to ν and σ_p and not to N_t (Figure F.4).

7.3.5 Relationships with gamebird release density

There were only five estates (CUL, HIR, NOG, NYP, VAR) with overlapping FMS and NGC data for years 1996-2000. The release density of gamebirds (pheasant and red-legged partridge) on these estates ranged from 3 birds km⁻² (VAR) to 959 birds km⁻² (NYP). Pheasants were released at densities ten times higher than red-legged partridges. Although not significant at $P < 0.05$ due to the low number of estates, there were positive relationships between both posterior median immigration rate and carrying capacity estimates with mean gamebird release density, with immigration rate and carrying capacity both higher on estates where there was more releasing (Figure 7.15a, Figure 7.16a). These relationships were similar with both mean gamebird bag density and density of gamebirds not shot in each year (Figure 7.15b,c, Figure 7.16b,c). There was a positive relationship between *per capita* birth rate and release density, but this was only with red-legged partridge and not with pheasants.

7.4 Discussion

7.4.1 Parameter estimates

This Chapter estimated the parameters determining within-estate fox population dynamics using Bayesian state-space modelling. For some parameters, including immigration rate and carrying capacity, these represent the first known estimates in any fox population. The number of estates for which there was enough data for reliable estimation was unfortunately less than one-third of the 75 estates that contributed to the FMS. The other two-thirds either did not contribute three or more years of data or had periods of missing data longer than nine months. The parameter estimates obtained from the 22 estates

modelled were nevertheless revealing about the relationship between the cull and within-estate fox population dynamics, and about the differences in these dynamics between different estates. The 22 estates were not distributed evenly across Britain and were instead located in only a few regions and landscapes. There was also more than expected spatial variation in local parameter estimates, meaning that modelling the data within a hierarchical structure was not explored further. The spatial variation is discussed in relation to gamebird releasing below.

Posterior distributions for model parameters showed considerable updates from the priors on most estates. Non-culling mortality was the parameter which showed the least updates and the posteriors for M were sensitive to the choice of informative prior specified in Chapter 5, supporting the findings from the simulation-estimation study that M is weakly identifiable using this model. The use of alternative informative priors for M did not affect the fox density estimates though, which were similar under either prior. There was no relationship between posterior median estimates of M and estate size, indicating the implicit emigration rate component of M was minimal as it was expected that smaller estates would have higher values of M if emigration was large. The posterior median estimates of M did show the only suggestion of spatial clustering for any parameter as the highest estimates were in the east and the lowest estimate was in the west. This could potentially reflect differences in regional temperature that may affect survival. Most of the estates were located in East Anglia and in South West England, and although mean annual temperatures were similar in these regions the winter period was on average 0.5°C cooler in East Anglia during 1996-2000 (Met Office 2011). This fits the pattern in estimates, but for foxes, whose range covers the northern hemisphere above the Arctic Circle (Macdonald & Reynolds 2004), this small difference really is unlikely to severely affect survival.

Immigration rates were mostly updated to median values higher than the prior for ν . This suggests that any bias from the assumptions made in constructing the informative prior for ν in Chapter 4 did not influence the results. The updating to higher values can be explained by the location of the modelled estates, which were predominantly in arable and pastoral landscapes and not uplands. The posterior median ν estimated for arable and

pastoral landscapes in Chapter 4 were higher than the median of the posterior predictive distribution upon which the prior was specified, which accounted for all landscape types. It was therefore to be expected that the immigration rates estimated on these estates might be higher than the prior, but the size of the immigration rate on some estates was particularly high. The immigration rate parameter is a maximal rate, reflecting the maximum number of foxes that would move onto the estate if the fox density was maintained near zero throughout the year. The highest estimate for ν , on YEM, was equivalent to about 29 foxes $\text{km}^{-2} \text{yr}^{-1}$. This estate is located in the pastoral a landscape, but the location can explain the size of the ν estimate as it had a large urban area on one boundary and a forested national park where there was limited fox control on the other. High immigration pressure could thus be expected here as both of these habitats act as source populations of foxes (Trehwella, Harris & McAllister 1988; Baker & Harris 2006).

The use of a *per capita* birth rate parameter to model the recruitment of weaned cubs meant that if the number of cubs weaned was to equal the number of cubs born then it was assumed that there was no pre-weaning non-culling mortality of cubs within earths. Most of the posterior median estimates for r were lower than the prior median. A consequence of using litter size per female data to specify the prior for r (Appendix D) was that posterior estimates of r could be updated to lower values relative to the prior either because the *per capita* birth rate was lower on an estate or because there was within-earth mortality of cubs. Without information on within earth mortality it was not possible to separate these two effects. This is not a problem *per se* as the modelled process was the recruitment of weaned cubs, but interpretation of the parameter estimates as *per capita* birth rates for comparison with other studies must be performed with care.

The level of posterior updating for r was variable but on most estates the median estimates were similar or slightly lower than the median of the informative prior, indicating that the prior was having an influence on the results. Indeed, the posteriors for r were sensitive to the choice of prior, but the fox density estimates were similar using either the informative prior based upon litter size data or the vague uniform prior with an upper bound at maximum litter size. This is because the central tendency under both priors was similar, at

around 3 cubs fox⁻¹yr⁻¹. The posteriors for r on HIR showed the most similar results under either prior choice. This may be explained by the large number of cubs killed at earths on this estate which meant there was more information about how many cubs must have been born.

The lowest estimate for r was on VAR and was 1.16 cub fox⁻¹yr⁻¹. This suggested significant within-earth non-culling mortality before cubs were weaned on this estate. There were very few cubs culled at earths on this estate despite a high level of control by lamping and other methods. The recorded cull of cubs may have been small either because little effort was put into it or because there were few cubs to cull; this is unknown. The use of fumigants to kill cubs within the earth cannot be ruled out. The fox population on this estate was low and appeared to be heavily suppressed. It could be that due to the intensity of control vixens were being killed following birth of cubs, causing mortality of the dependent cubs within the earths. Culling during the spring and summer, while being especially effective at this time, does carry a welfare cost of failing to locate and destroy orphaned cubs (Reynolds 2000). VAR was a very large estate and so considerable effort would have been required to find all of the breeding earths across it.

The posteriors for the rate of successful search were consistently updated to lower values than the prior. The informative prior was specified using data from a distance sampling survey conducted along tracks from standing in the back of a vehicle, which was assumed to represent how many gamekeepers perform lamping (Chapter 6). Lamping may also be performed cross-country from a quad bike or on foot. This would cause d to be lower. Under both of these methods, the speed of travel is likely to be significantly lower than along tracks from a vehicle. Also, the field of view will be smaller as the observation position will be lower. Without data on the lamping methods used by each gamekeeper it is not possible to quantify this, different lamping behaviour from that assumed under the prior seems the most reasonable explanation for lower estimates for d .

The simulation-estimation study in Chapter 3 indicated that datasets with higher annual variation in effort (0.1 to 2.5 times the mean weekly lamping effort) had the least biased and most precise parameter estimates. Examining the CV of parameter estimates

from individual estates relative to the mean CV for each parameter across estates suggests that there was no relationship between the variation in year-to-year lamping effort and the CV of the parameter estimates. However, few estates showed similar annual variations in mean weekly effort and so an in-depth analysis was not possible. The largest variation was seen on LEL, where annual effort varied from 0.6 to 1.8 times the mean weekly effort, but here the CV of parameter estimates was above the mean CV for all parameters except N_0 . The data from LEL perhaps explain this lack of precision. Around one-quarter to one-half of weeks in the time series had lamping effort, but the mean weekly effort was the lowest of all estates (0.4 hr wk^{-1}) and the vast majority of weeks saw zero fox sightings and consequently few foxes killed. In contrast, the maximum sighting rate was over six foxes seen per hour. This variation in sighting rate caused large observation errors and consequently low precision in estimates.

In contrast, the estate with the highest mean weekly effort was VAR (10.4 hr wk^{-1}) where year-to-year variation was lower (0.8 to 1.2 times). CV was lower than mean CV for all parameters except r and K on this estate. The only estate where CV was lower than mean CV for all parameters was GHT, which had one of the highest effort levels (5.57 hr wk^{-1}) but only minimal year-to-year variation (0.9 to 1.1 times mean weekly effort). These results suggest that precision of results is more dependent upon the amount of lamping effort than the variation in effort, but further work to examine the effect of larger effort variation on estates where there is more effort is required.

7.4.2 Effect of culling on fox density

The estimates of fox density show that culling suppressed the population relative to estimated carrying capacity on all estates, with pre-breeding density on average 43% of K . Culling therefore appears to have at least halved the food requirements of the fox population relative to the no-cull situation on most estates, and so in this respect, this amount of culling must be considered a success. Nevertheless, despite some large culling efforts few estates were able to consistently achieve low fox densities throughout the year, which may have important implications for food requirements and therefore prey populations. The most

likely explanation for this failure to reduce local fox density further was high immigration rates, as has previously been suggested (Reynolds, Goddard & Brockless 1993; Baker & Harris 2006). VAR achieved the most consistently low fox density, but this came at a cost of some 540 hours of lamping per year which was by far the biggest investment. Immigration onto this estate was also at a relatively low rate. Under the most likely reconstruction of fox density, as determined by the posterior median, no estate had zero fox density throughout the bird nesting period between March and July, although this was achieved for a couple of weeks on DLQ, GHT and HIR. Despite above average immigration rates, these estates used above-average levels of lamping effort. The lower credible intervals for fox density on these estates did include zero for longer, but not for periods longer than 3 months during the nesting period.

Failure to achieve high suppression of the pre-breeding fox population, or not achieving low fox density during the bird nesting period does not mean that the control was ineffective on those estates. An evaluation of the culling effectiveness can only be performed with respect to the aims of fox control on each estate. The precise aims of control were unknown for nearly all estates. One estate, DLQ, is of special interest because it was the site of a high-profile demonstration of ‘wildlife-friendly farming’, using game management techniques including predator control (Boatman & Brockless 1998; Stoate, Brockless & Boatman 2002; Stoate & Leake 2002). Intensive study at this site, and on comparison sites nearby, contributed to evidence that common predators can limit the density of some prey species (Stoate & Leake 2002; Reynolds *et al.* 2010b; White *et al.* 2014). The role of foxes within this effect will therefore be of interest to many as a case study. The detailed monitoring of small game populations on this estate allows comparison of their population dynamics with the reconstructed dynamics of fox density. Beginning in 1993, control of foxes and corvids was implemented during the spring and summer. Autumn counts of pheasants and hares showed that these prey populations had recovered significantly by the start of the FMS in 1996, and continued to remain high through 2000 until predator control was stopped on the estate in 2001. Despite the pre-breeding suppression of foxes only being about 53%, and fox density not being zero during the nesting period, prey populations were flourishing and these observations offer support for the notion that the

culling effort was achieving its aims. The results from DLQ indicate the importance of targeting culling effort before and during the bird nesting period to improve productivity.

The data from DLQ provide anecdotal support for the reconstruction of fox density on this estate (Stoate & Leake 2002). In 1997 the prey populations of both pheasant and hare dropped, and pheasant breeding success also fell sharply, before recovering in 1998. At the time, the drop in 1997 was attributed to wet weather during June, but the weather in June 1998 was not much better as despite fewer rain days the total rainfall was higher (Anon 1999). The role of predation was not considered in the recovery, but the FMS data show that during spring/summer 1997 there were fewer foxes killed and no cubs killed at earths. The fox density was consequently high during 1997, which indicates that predation and weather are both related to pheasant and hare productivity. Culling effort was similar in 1998 but three times as many foxes were killed, including a large number of cubs at earths. Cub recruitment was therefore minimal and the predation pressure on prey populations during the nesting period was much reduced as fox density declined to zero by the end of July. Fox density increased when control ended for that year but pheasant breeding success had been allowed to recover despite the poor weather and so autumn counts recovered to 1996 levels (Anon 1999).

The number of foxes killed was shown to be a poor indicator of culling effectiveness, as VAR had one of the lower number of foxes removed per km² but the effort was highly effective at suppressing density year-round. The low number killed simply reflected the lower density of foxes available to cull, which is a problem with the use of bag data where effort is not measured (McDonald & Harris 1999; Reynolds 2000; Sadler *et al.* 2004). The scale and frequency of effort were better predictors of effectiveness. DLQ, GHT, HIR and VAR all used above average levels of lamping effort, which was either used consistently throughout the year or targeted before and during the bird nesting period. These estates achieved the lowest fox densities during this period. However, simply examining effort is not enough as FHC and YEM also used high levels of effort but failed to achieve much impact on fox density due to the immigration rate on these estates being the highest two

estimated values. This highlights the need for the model-based approach to understand the importance of different population processes on each estate.

Density dependence was a feature built in to the model and a property of the logistic terms used to model it is that the number of cubs recruiting and the number of foxes immigrating into the population are maximised at 50% of K . In harvesting models, this is the density at which maximum sustainable yield is achieved (Williams, Nichols & Conroy 2002). Lethal pest control can be viewed as harvest of sufficient intensity to reduce a population, but because of density dependence pest control might simply exact a sustained yield from a population (Guthery & Shaw 2013). Ten of the 22 estates had pre-breeding fox densities in the range of 40-60% of K and so appear to have been removing a close to maximum harvest of foxes from the population rather than achieving effective control. Increased culling effort, or targeting of effort at more effective times, is required on these estates to overcome the density-dependent response.

An example of this effect is found in the response to control on YEM. Culling mortality on this estate was over $10 \text{ fox km}^{-2}\text{yr}^{-1}$, which was the highest of all estates. Even with large culling effort and a large cull, fox density was high relative to carrying capacity throughout the year and control was relatively ineffective. The high immigration rate ($29 \text{ fox km}^{-2}\text{yr}^{-1}$) meant that at the fox density estimated on YEM, which was on average 68% of K , the cull was essentially harvesting immigrant foxes and having no effect on the resident breeding population. Density-dependence means that as fox density approaches zero, the maximal number of immigrants will be expected to move onto the estate. To suppress fox density on this estate even more intensive culling effort would be required. The effect of immigration rate on the level of control required can also be seen by comparing the results on HIR and VAR. The mean fox density on these estates was similar at around 1 fox km^{-2} and so was estimated carrying capacity at around 3 fox km^{-2} . To maintain the same fox density, the annual cull on HIR had to be twice as large as on VAR due to higher immigration and *per capita* birth rates.

7.4.3 Relationships with gamebird releasing

There was a notable lack of local similarity in parameter estimates. Parameters such as carrying capacity, immigration rate and per capita birth rate were expected to be more similar on estates sharing habitat features and fox culling pressures within regional landscapes, but the relationships found between these parameters and gamebird release densities suggest that local variation in food availability is an important factor in fox population dynamics on restricted areas. Release of hand-reared Galliformes species such as pheasant and red-legged partridge is a common practice in Europe and North America (Sokos, Birtsas & Tsachalidis 2008). In Britain, the practice of releasing birds has increased greatly in recent decades. Since 1961 the NGC index of pheasant released has increased nine-fold and the increase for partridge has been almost exponential (Aebischer 2013). The most recent estimate was that 35m pheasants and 6.5m partridges were reared and released for shooting in 2004 with return rates of 40-43% (PACEC 2006). High populations of birds made possible by releasing are known to be a valuable food resource for foxes (Reynolds & Tapper 1993), which in the absence of effective fox control may attract substantial predation (Reynolds 2000). From these results gamebird releasing apparently increases the carrying capacity of an estate for foxes, attracts an increased rate of immigration to replace culled foxes, and possibly also increases cub production. However, it must be stressed that these relationships are based upon only five data points and so are not conclusive, merely suggestive. The precision of the parameter estimates must also be taken into consideration, together with the reliability of the estimates. Results from the simulation-estimation study show that although bias in parameters was low, immigration rate was the least-biased of these parameters and so the highest level of confidence is in the relationship of ν with gamebird release density. Gamebird releasing data was asked for retrospectively for all of the remaining 17 estates which were not part of the NGC, but data were not forthcoming from any other estates.

An important point is that on these five estates the effect of gamebird releasing on within-estate fox density was not counteracted by effective fox control. The estate with the highest density of released birds, NYP, was the least-suppressed fox population of all 22

estates modelled. The increase on NYP during winter 1998 to a fox density above carrying capacity coincided with the lowest return rate of pheasants over the 1996-2000 period, suggesting that the increased food availability may directly facilitate higher fox numbers. In contrast, the estate with lowest density of released birds, VAR, had one of the higher levels of suppression. More than twice as much lamping effort was used on VAR compared to NYP, but the bag of foxes on NYP was more than twice as large. On estates releasing more birds, fox control therefore appears to be harder as there are more foxes, but less culling effort goes into it.

The estimates of pre-breeding fox density were generally higher than predicted based upon the landscape type, with only six estates (CIP, FAH, HIR, LEL, RAM, VAR) being within the range of estimates based upon faecal density counts (Webbon, Baker & Harris 2004). All of these estates achieved above average suppression of the fox population. Of those estates that were within 0.1 fox km^{-2} of the landscape means, HIR and VAR had the lowest densities of released gamebirds. Landscape has previously been shown not to be a good predictor of fox density (Heydon, Reynolds & Short 2000). A potential explanation for the fox density on other estates being higher than expected based upon landscape could therefore come from the unknown density of gamebirds on these estates, which on shooting estates are likely to be higher due to habitat management and control of other predators. On estates where releasing occurs, densities of gamebirds will be a lot higher and the birds more naïve than wild stocks, which could support many more foxes. Fox control on neighbouring estates at levels lower than the regional average may also contribute to higher fox densities as the local pool of potential immigrants will be larger. Knowledge of neighbouring control was lacking for most estates modelled, though on DLQ the high estimates for both v and N_t were unsurprising as it was known that there was no fox control in the surrounding area (Boatman & Brockless 1998).

7.4.4 Assumptions

Other than the sensitivity to prior distributions for r and M , there were some important results from the examination of the sensitivity to structural and process error

assumptions made by the model. The distribution of the timing of fox breeding events appeared to adequately capture the variation in timing of recruitment of weaned cubs as there was minimal effect of the mean recruitment date being two weeks earlier or later. The onset of breeding occurs in late-winter and is correlated with day length, starting earlier at more southerly latitudes (Lloyd & Englund 1973). The two fox populations used to establish the distribution were in Wales and south-east England (Lloyd 1980). These regions are on similar latitudes and given that most of the estates were within this range they would be expected to have similar timing of breeding events.

The model made the assumption that immigration rate was constant over time rather than seasonal. The results were not sensitive to alternative assumptions about the seasonality of immigration rates as there were minimal effects on estimated fox density. Although slight differences in fox density were found on some estates under seasonal immigration, resulting from differences in the ν , K and d parameter estimates, the direction of the differences were not consistent between estates. If movement were seasonal, ν would be underestimated by assuming it were constant. Of the six estates examined, the seasonal estimates of ν were higher relative to the constant model on NYP and VAR, but lower on all other estates. The assumption of constant immigration also implies that conditions on each estate, e.g. food availability, were constant, and also that conditions in the neighbouring areas were similar during the FMS period, i.e. they did not end or begin fox control. These details and the possible effect on the estimations were unknown.

In a state-space model, unexplained variation in fox density due to environmental and demographic stochasticity is modelled using process error deviates. The incorporation of process error on two-weekly time steps has the potential to allow too much variation in the population due to environmental effects as these are more likely to vary and affect population growth annually. However, when demographic effects are considered, in particular exceptional immigration events such as whole family groups moving onto an estate which can occur over short time periods, this shorter time step is required. The choice was made to fix the standard deviation in process errors at 0.2 to reduce identifiability problems associated with estimating this parameter. Under smaller fixed values for σ_p , the fit of the

model through sighting rate failed to capture any variation in sighting rate, with the credible interval for predicted sighting rate omitting many of the observed data points. Consequently it was more difficult to achieve model convergence under smaller values of σ_p and reconstructed fox density took unrealistically high values, particularly on DLQ where mean fox density under σ_p of 0.05 was 5.50 fox km⁻². The empirical estimates of σ_p suggest that while the model required a value of 0.2 to converge onto the joint posterior, the realised variation in N_t caused by process error was within the range permitted by the model. Similar to other parameters there was considerable spatial variation in empirical σ_p estimates across estates, with no obvious regional pattern. When σ_p was estimated using a uniform prior there were some very high estimates on some estates. Elevated estimates of process and observation variance may suggest errors in model specification that could lead to biased estimates (Thorson, Ono & Munch 2014). However, the highest estimate of σ_p was on VAR, an estate on which lamping was conducted almost every week for the entire length of the five-year FMS period; this result is consistent with the finding of a study on ungulates where Bayesian process error variance increased with time series length (Ahrestani, Hebblewhite & Post 2013).

7.5 Tables

Table 7.1. Mean estimates of annual process error standard deviation σ_p from terrestrial species. Ranges of values indicate estimates obtained either from more than one population or from using alternative estimation methods

Species	σ_p	Reference
Mammals		
Red deer/Elk <i>Cervus elaphus</i>	0.0003-0.14	Ahrestani <i>et al.</i> (2013)
Reindeer/Caribou <i>Rangifer tarandus</i>	0.003-0.25	Ahrestani <i>et al.</i> (2013)
Wolf <i>Canis lupus</i>	0.08	Liberg <i>et al.</i> (2012)
Sika deer <i>Cervus nippon</i>	0.22	Iijima <i>et al.</i> (2013)
Red kangaroo <i>Macropus rufus</i>	0.28	Knape <i>et al.</i> (2011)
Birds		
Eurasian sparrowhawk <i>Accipiter nisus</i>	0.07	Hosack <i>et al.</i> (2012)
Greater snow goose <i>Chen caerulescens atlantica</i>	0.10-0.14	Lebreton & Gimenez (2013)
Ovenbird <i>Seiurus aurocapilla</i>	0.11-0.18	Knape <i>et al.</i> (2013)
Puerto-Rican parrot <i>Amazona vittata</i>	0.12	Hosack <i>et al.</i> (2012)
Canvasback <i>Aythya valisineria</i>	0.14	Gimenez <i>et al.</i> (2009)
California condor <i>Gymnogyps californianus</i>	0.21-0.30	Hosack <i>et al.</i> (2012)
Scaly-naped pigeon <i>Patagioenas squamosa</i>	0.25	Rivera-Milan <i>et al.</i> (2014)

Table 7.2. Estate area, number of contributed weeks' data, number of weeks of lamping effort and annual lamping effort per km²

Estate	Area (km ²)	Total weeks in culling period (weeks with lamping effort)					Annual lamping effort (hr km ⁻²)				
		1996	1997	1998	1999	2000*	1996	1997	1998	1999	2000*
BMM	3.6	-	-	40 (10)	52 (13)	35 (12)	-	-	7.2	11.2	9.6
CHU	3.6	-	-	40 (23)	52 (31)	35 (12)	-	-	14.5	17.1	8.3
CIP	2.4	52 (23)	52 (17)	52 (15)	13 (5)	-	16.3	12.8	12.0	6.6	-
CUL	20.2	52 (26)	52 (21)	52 (15)	52 (13)	14 (3)	5.2	4.0	2.4	1.8	0.6
DLQ	3.2	40 (6)	52 (14)	52 (13)	52 (12)	35 (9)	5.1	13.4	12.2	11.3	11.3
DWS	18.2	-	40 (24)	52 (39)	36 (18)	-	-	9.6	17.6	6.3	-
EWE	4.9	52 (26)	52 (28)	52 (29)	52 (24)	35 (15)	7.8	7.8	7.5	6.2	4.2
FAH	5.4	-	-	40 (12)	52 (17)	35 (8)	-	-	2.4	5.4	3.4
FHC	4.1	52 (41)	52 (36)	52 (37)	52 (31)	35 (19)	32.0	29.2	23.3	29.8	11.0
GDE	36.4	52 (29)	52 (26)	52 (23)	52 (21)	35 (16)	3.2	2.9	2.3	1.7	1.3
GHT	5.7	-	-	40 (38)	52 (49)	35 (34)	-	-	35.7	49.5	38.1
HIR	6.1	-	-	40 (38)	52 (52)	35 (35)	-	-	43.7	59.3	31.5
HUS	9.3	52 (18)	52 (15)	52 (26)	52 (26)	35 (14)	5.8	4.5	12.0	11.2	3.6
LEL	2.4	52 (29)	52 (12)	52 (25)	13 (6)	-	15.7	5.2	8.3	1.4	-
MAH	4.9	52 (14)	52 (15)	35 (6)	-	-	7.1	11.3	3.8	-	-
NOG	8.1	-	40 (29)	52 (35)	52 (38)	35 (13)	-	11.6	10.9	18.6	5.6
NYP	10.1	52 (17)	52 (20)	52 (37)	35 (23)	-	4.4	3.4	8.1	6.2	-
OCS	1.6	52 (31)	52 (21)	52 (28)	13 (4)	-	24.8	15.8	24.9	2.2	-
RAM	2.4	52 (17)	52 (16)	52 (28)	52 (24)	35 (14)	5.3	9.6	12.0	9.8	6.4
VAR	24.3	52 (45)	52 (52)	52 (52)	52 (51)	35 (35)	17.6	21.3	21.8	27.0	15.8
VDL	4.0	40 (22)	52 (27)	52 (16)	52 (14)	35 (10)	18.3	24.8	17.0	13.7	9.4
YEM	4.3	31 (23)	52 (25)	52 (27)	52 (18)	35 (17)	20.9	16.8	20.5	13.5	12.8

*max of 35 weeks (to 31 August 2000)

Table 7.3. Prior probability distributions for estimated model parameters

Model parameter	Units	Distribution	Parameters
N_0	fox km ⁻²	~ uniform	lower = 0.001 upper = 13.9
K	fox km ⁻²	~ uniform	lower = 0.001 upper = 13.9
ν	fox km ⁻² 2wk ⁻¹	~ lognormal	median = ln(2.41/26) CV = 0.84
r	cub fox ⁻¹ yr ⁻¹	~ gamma	$a = 7.66$ $b = 2.73$
M	2wk ⁻¹	~ lognormal	median = ln(0.469/26) CV = 0.59
d	km ² hr ⁻¹	~ lognormal	median = ln(2.00) CV = 0.56

Table 7.4. Posterior median (and CV) for estimated parameters on each estate.

Estate	N_0 fox km ⁻²	K fox km ⁻²	ν fox km ⁻² wk ⁻¹	r cub fox ⁻¹ yr ⁻¹	M wk ⁻¹	d km ² hr ⁻¹
BMM	2.68 (0.68)	6.82 (0.36)	0.107 (0.66)	2.94 (0.33)	0.0084 (0.59)	0.42 (0.30)
CHU	5.65 (0.52)	5.48 (0.34)	0.095 (0.64)	2.85 (0.32)	0.0079 (0.57)	0.31 (0.27)
CIP	0.74 (1.05)	4.80 (0.55)	0.036 (0.54)	2.62 (0.32)	0.0096 (0.62)	0.33 (0.29)
CUL	3.25 (0.51)	3.37 (0.48)	0.124 (0.69)	2.98 (0.38)	0.0086 (0.61)	0.52 (0.35)
DLQ	6.59 (0.37)	6.56 (0.36)	0.176 (0.60)	3.11 (0.36)	0.0086 (0.62)	0.20 (0.27)
DWS	1.65 (0.80)	4.80 (0.42)	0.170 (0.32)	3.46 (0.29)	0.0099 (0.70)	0.66 (0.28)
EWE	2.96 (0.54)	3.42 (0.42)	0.146 (0.39)	2.80 (0.35)	0.0085 (0.60)	0.71 (0.33)
FAH	0.80 (1.35)	2.27 (0.82)	0.049 (0.76)	3.19 (0.30)	0.0104 (0.69)	0.86 (0.36)
FHC	4.98 (0.40)	2.67 (0.41)	0.188 (0.50)	2.73 (0.38)	0.0075 (0.60)	0.19 (0.30)
GDE	2.19 (0.60)	2.57 (0.61)	0.100 (0.59)	2.75 (0.34)	0.0093 (0.62)	0.77 (0.36)
GHT	1.77 (0.63)	6.19 (0.42)	0.139 (0.32)	2.04 (0.30)	0.0085 (0.60)	0.20 (0.25)
HIR	0.24 (1.02)	2.74 (0.74)	0.140 (0.24)	2.99 (0.27)	0.0096 (0.68)	0.22 (0.23)
HUS	3.39 (0.57)	1.98 (0.67)	0.065 (0.58)	3.63 (0.32)	0.0102 (0.67)	0.36 (0.30)
LEL	1.11 (0.61)	3.79 (0.64)	0.024 (0.91)	2.36 (0.43)	0.0106 (0.64)	0.46 (0.41)
MAH	2.39 (0.41)	3.88 (0.53)	0.102 (0.35)	2.98 (0.35)	0.0092 (0.64)	0.63 (0.26)
NOG	1.83 (0.84)	4.90 (0.42)	0.082 (0.51)	2.68 (0.32)	0.0082 (0.59)	0.28 (0.27)
NYP	3.29 (0.62)	4.55 (0.42)	0.154 (0.75)	2.52 (0.36)	0.0070 (0.55)	0.42 (0.41)
OCS	0.96 (0.92)	8.47 (0.32)	0.063 (0.58)	3.32 (0.29)	0.0085 (0.58)	0.22 (0.28)
RAM	3.29 (0.55)	8.22 (0.32)	0.060 (0.80)	2.40 (0.36)	0.0082 (0.55)	0.39 (0.28)
VAR	3.89 (0.42)	3.34 (0.75)	0.036 (0.46)	1.16 (0.40)	0.0092 (0.61)	0.21 (0.29)
VDL	3.26 (0.43)	8.05 (0.30)	0.112 (0.64)	2.45 (0.37)	0.0070 (0.54)	0.29 (0.26)
YEM	1.89 (0.55)	6.30 (0.25)	0.561 (0.32)	1.92 (0.42)	0.0072 (0.58)	0.30 (0.25)

7.6 Figures

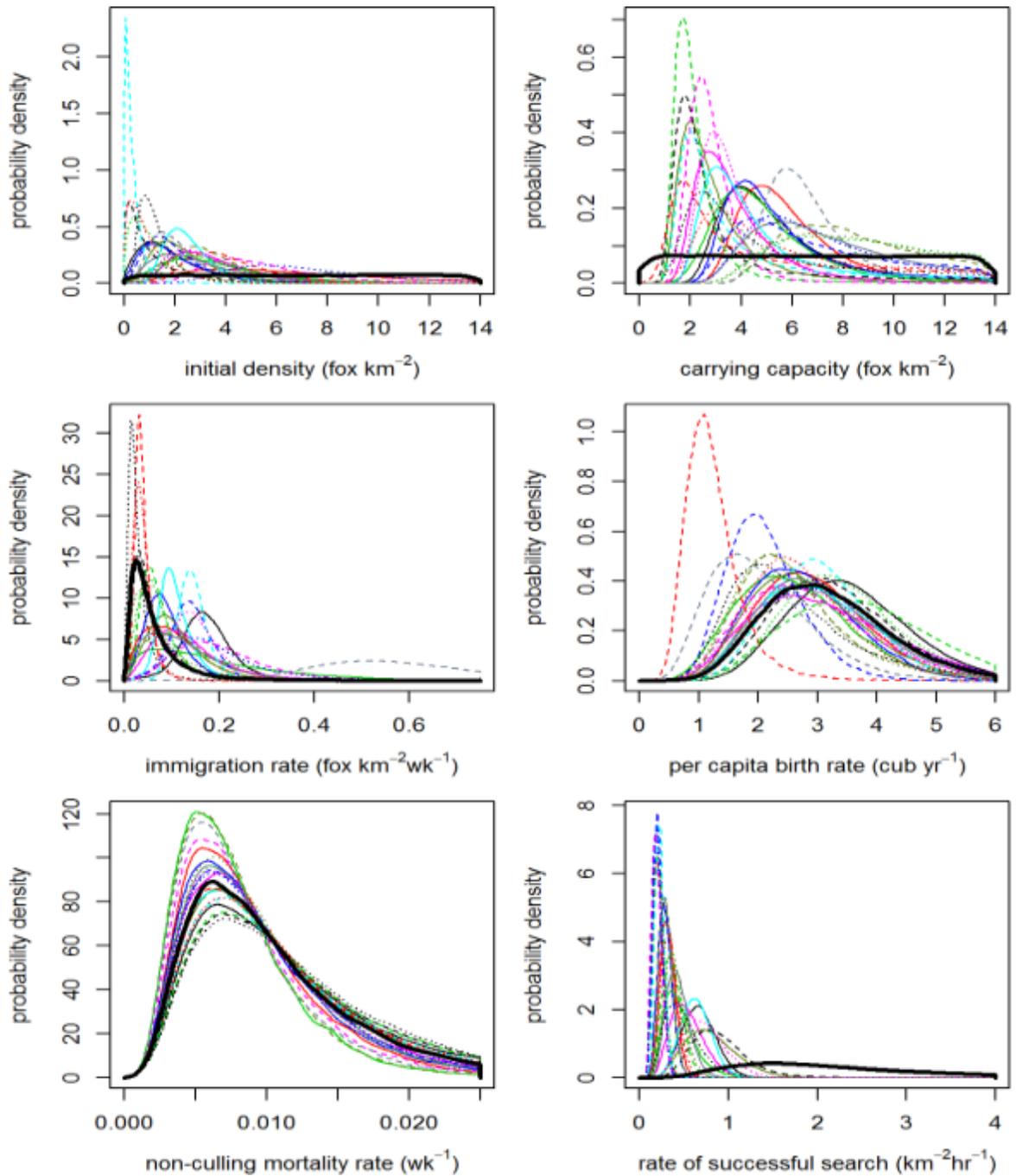


Figure 7.1. Marginal posterior probability distributions for the estimated parameters N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (non-culling mortality rate), and d (rate of successful search) from the 22 estates. Each line type and colour combination represents the same estate in each panel. The prior probability distribution for each parameter is shown by bold black line.

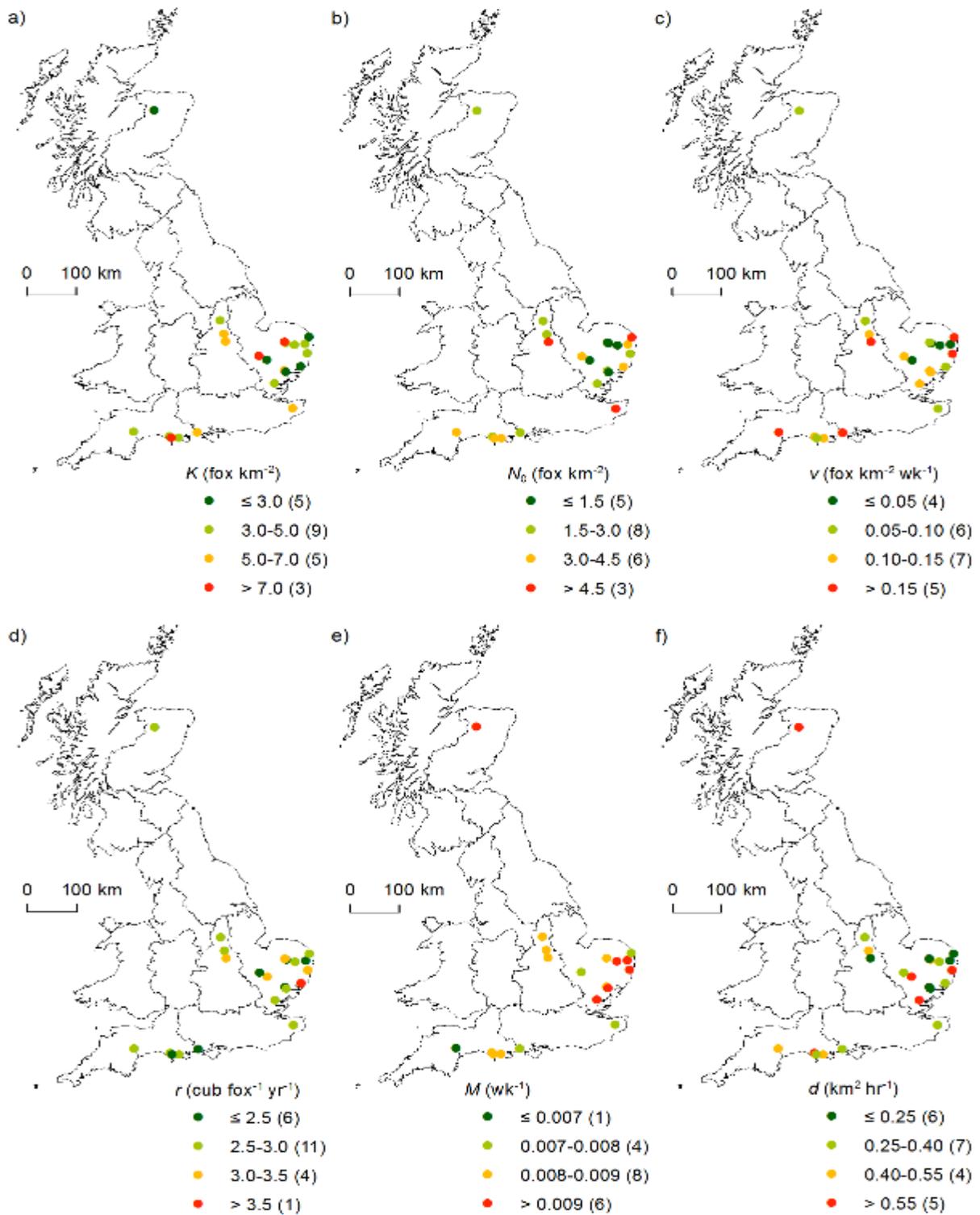


Figure 7.2. Spatial variation in posterior median estimates for a) carrying capacity (K), b) initial fox density (N_0), c) immigration rate (v), d) *per capita* birth rate (r), e) non-culling mortality rate (M), and f) the rate of successful search (d).

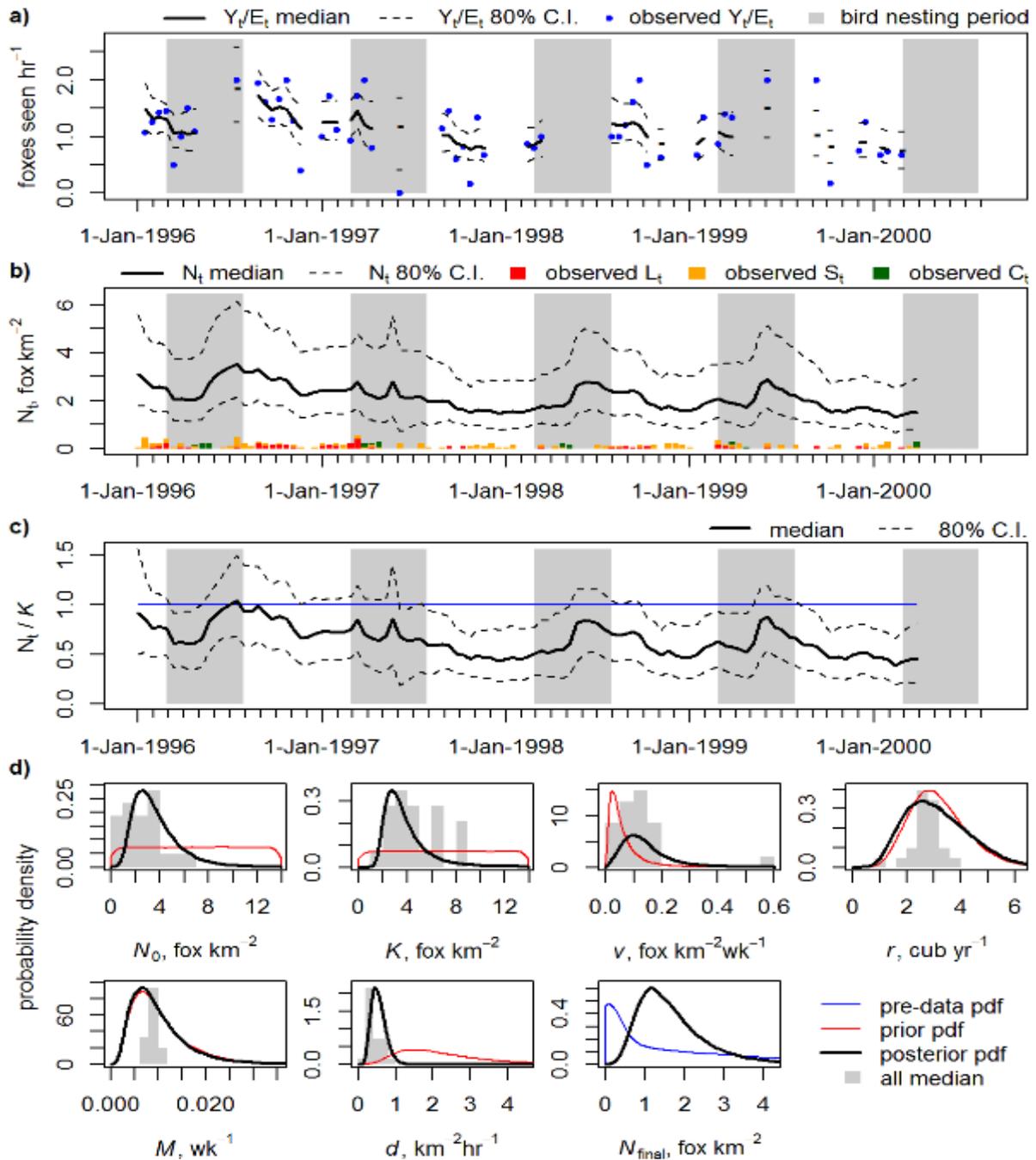


Figure 7.3. Results for CUL showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

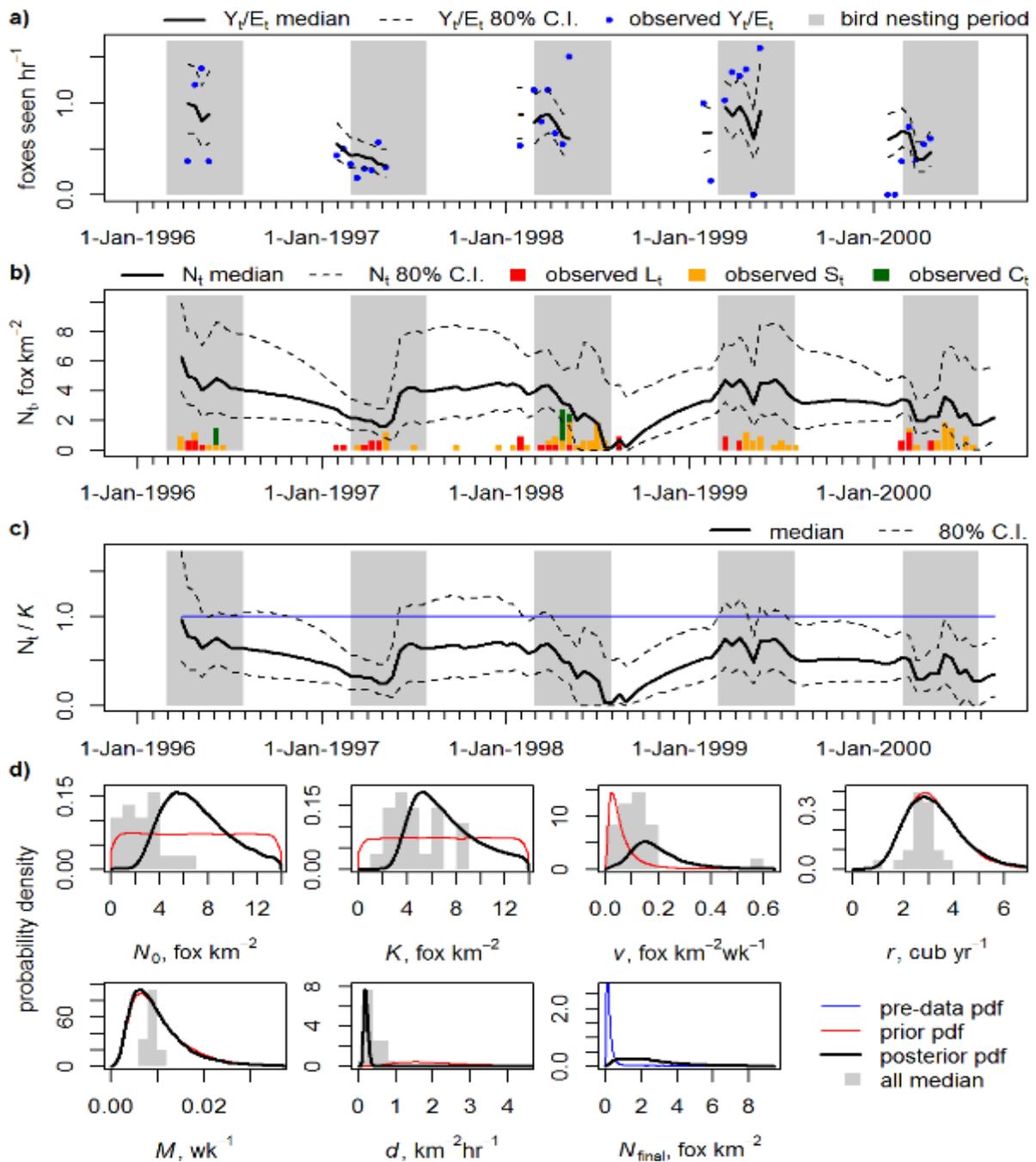


Figure 7.4. Results for DLQ showing a) posterior fit of the model to sighting rate (Y_i/E_i); b) posterior estimates of bi-weekly fox density (N_i) in relation to the cull removed by different methods; c) estimated N_i as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

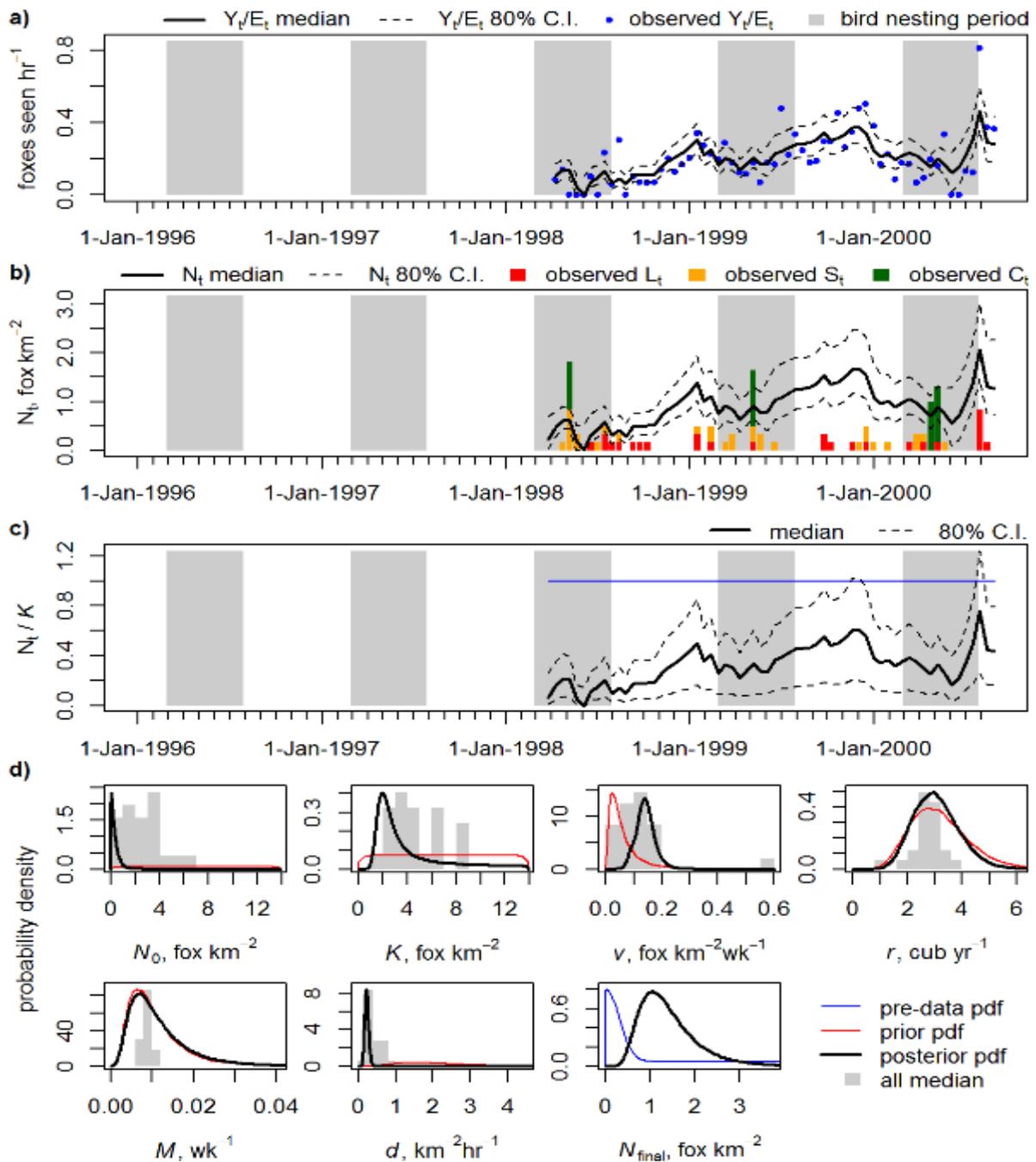


Figure 7.5. Results for HIR showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

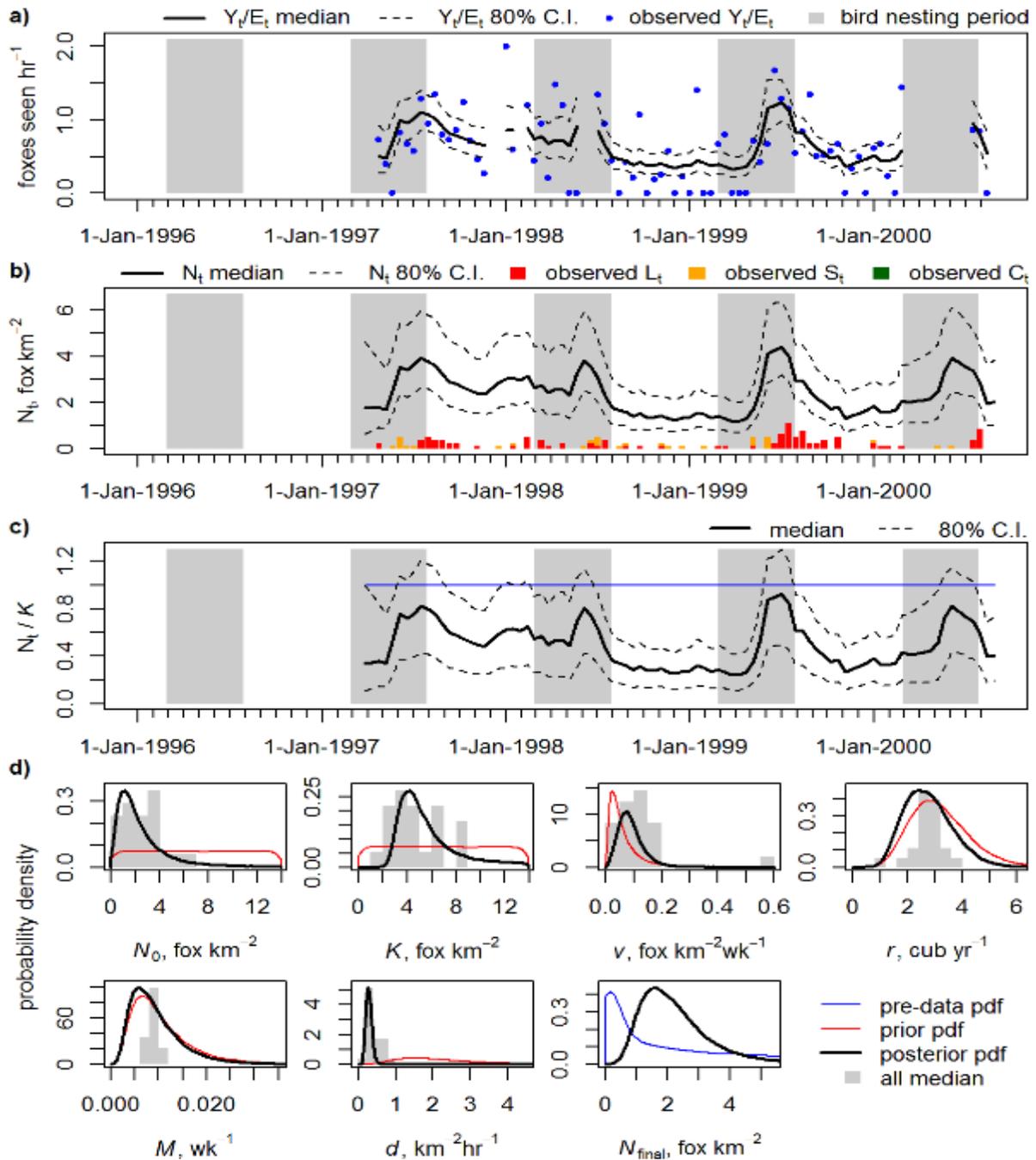


Figure 7.6. Results for NOG showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

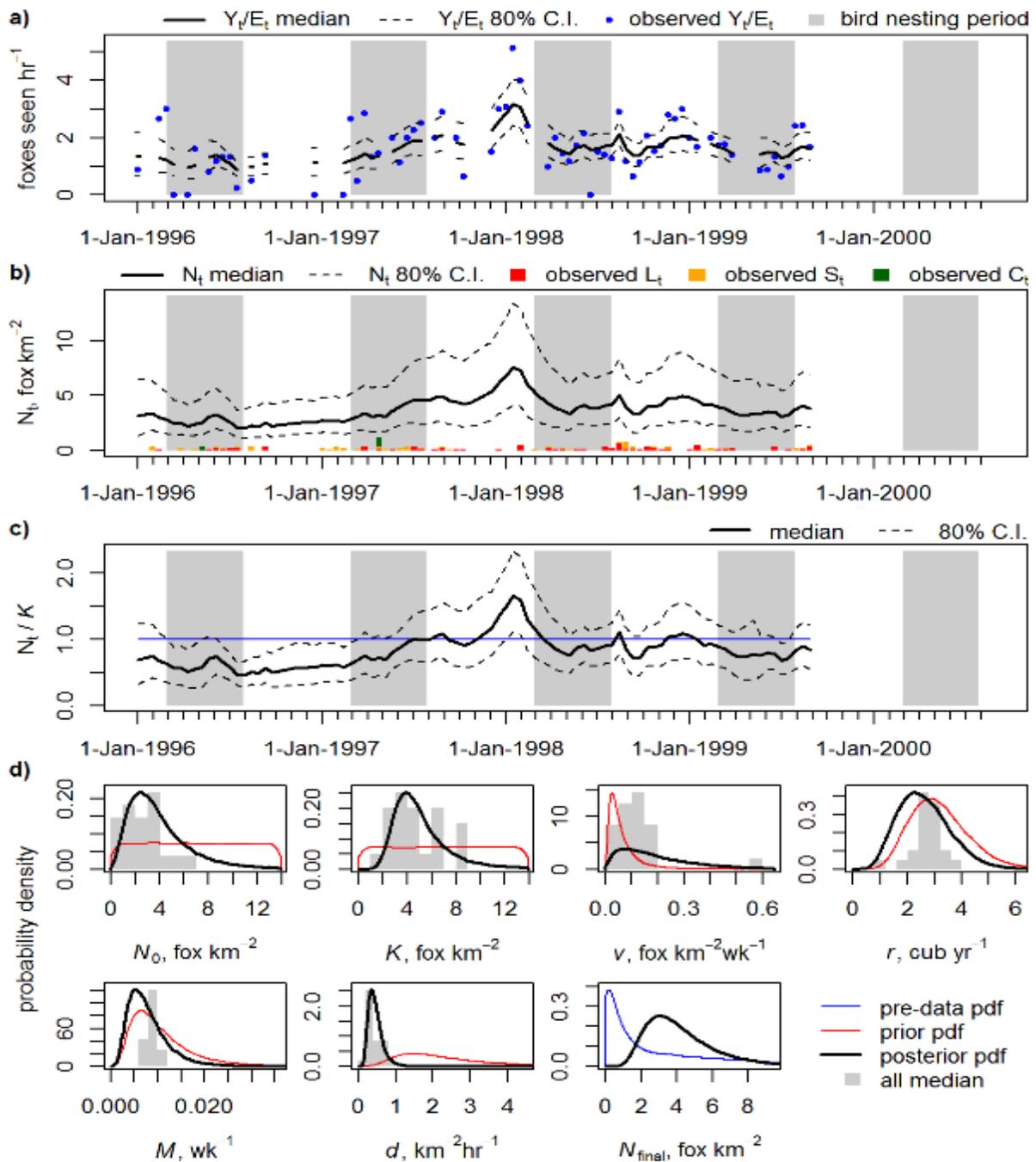


Figure 7.7. Results for NYP showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

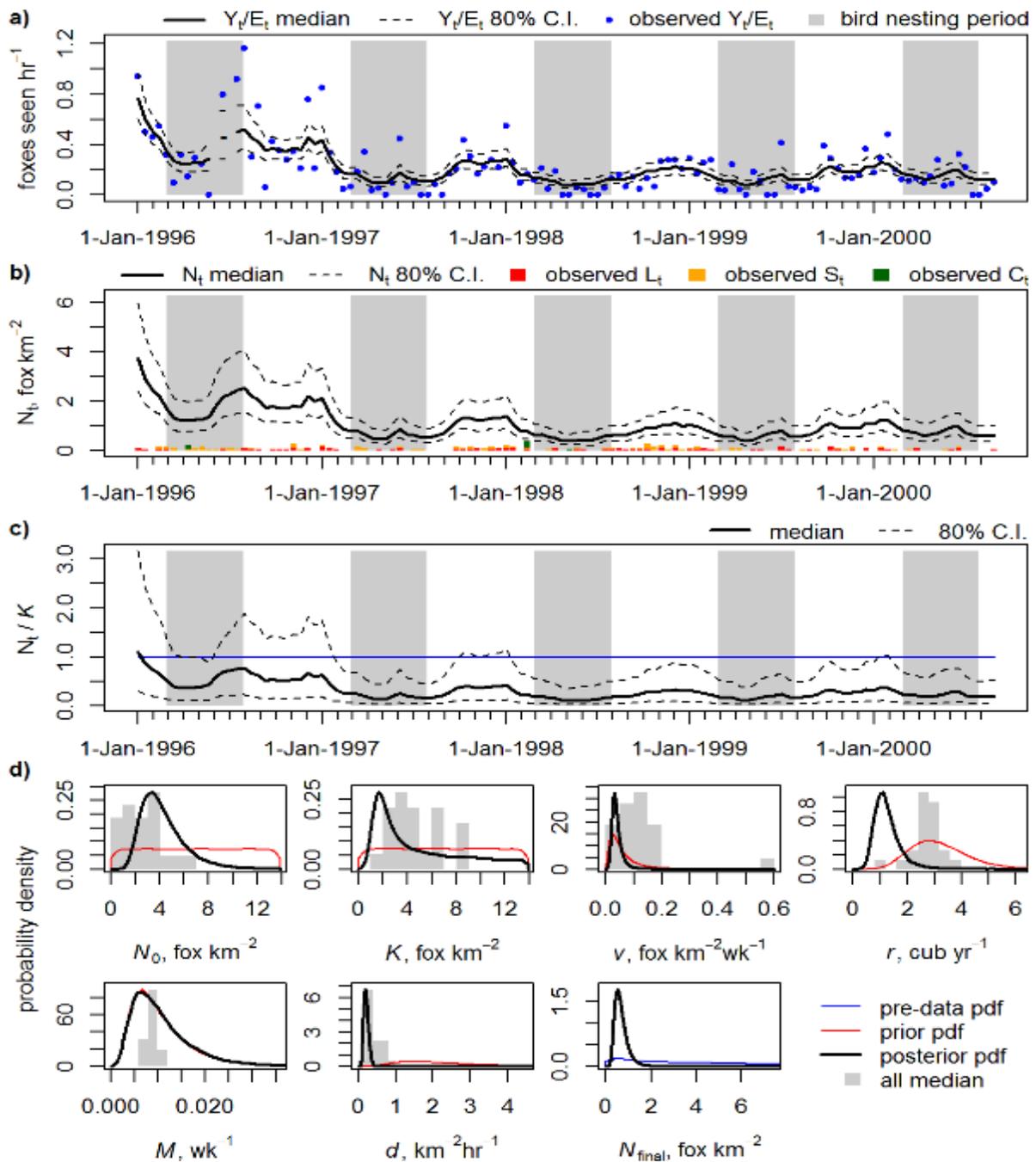


Figure 7.8. Results for VAR showing a) posterior fit of the model to sighting rate (Y_i/E_i); b) posterior estimates of bi-weekly fox density (N_i) in relation to the cull removed by different methods; c) estimated N_i as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

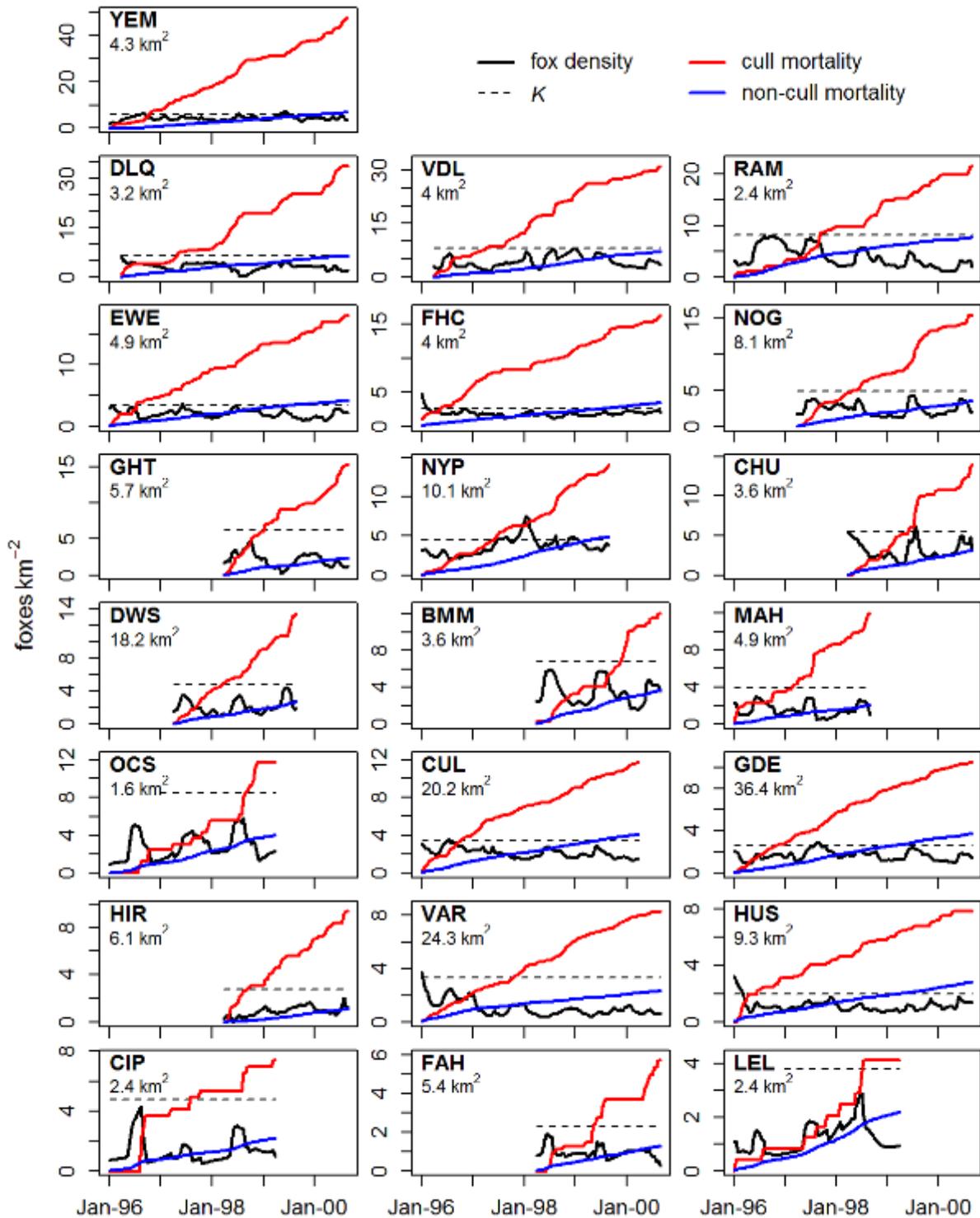


Figure 7.9. Comparison of the estimated culling mortality and non-culling mortality implied by the posterior median of M on each estate over the range of the contributed data. Posterior median fox density and carrying capacity of each estate are shown. The scale of mortality differed so estates are ordered by row from top-left to bottom-right by total mortality.

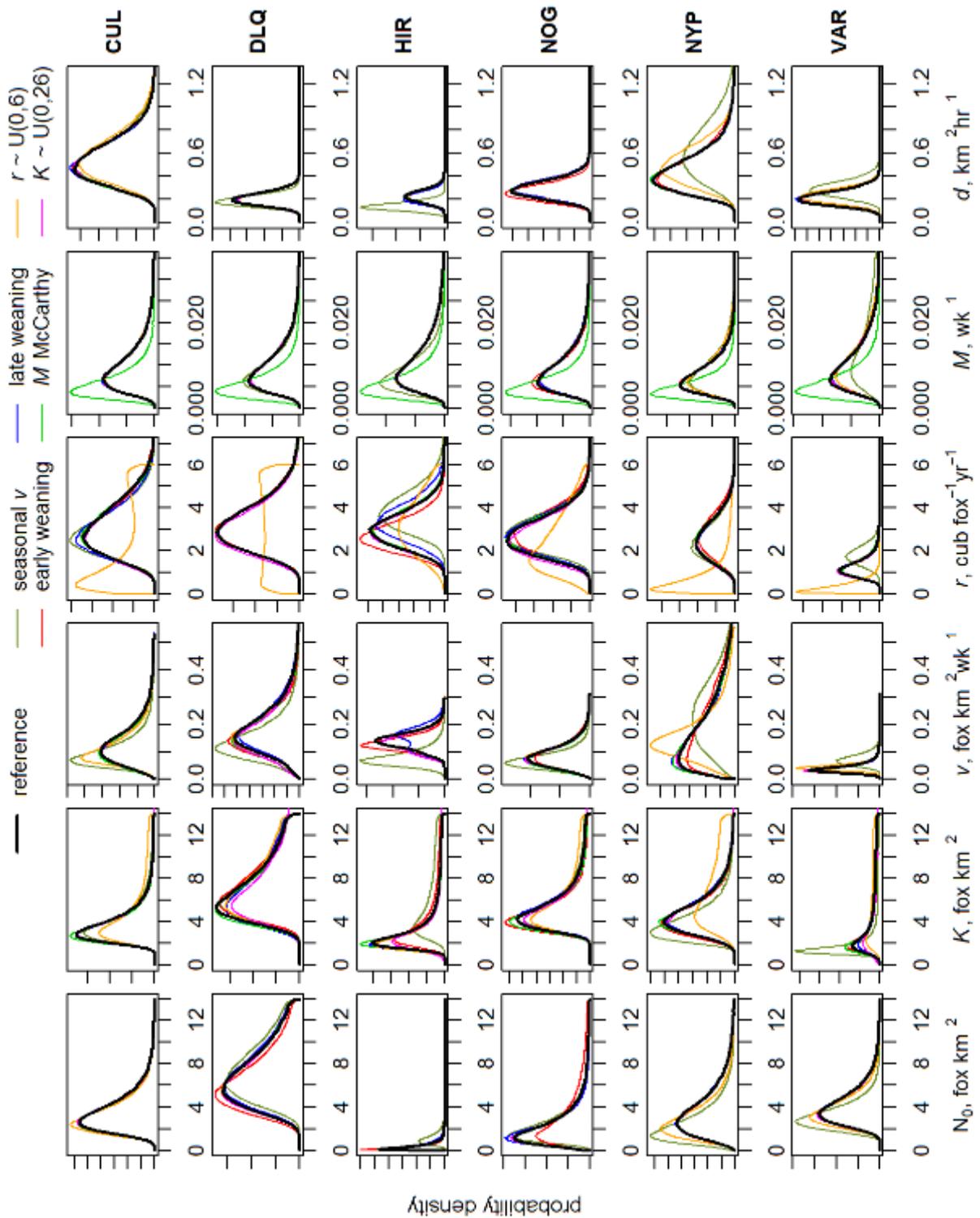


Figure 7.10. Sensitivity of marginal posterior distributions for parameters (columns) from six estates (rows) to different structural and prior distribution assumptions. The reference case distributions shown are from the informative prior model. The y-axes are not labelled for clarity.

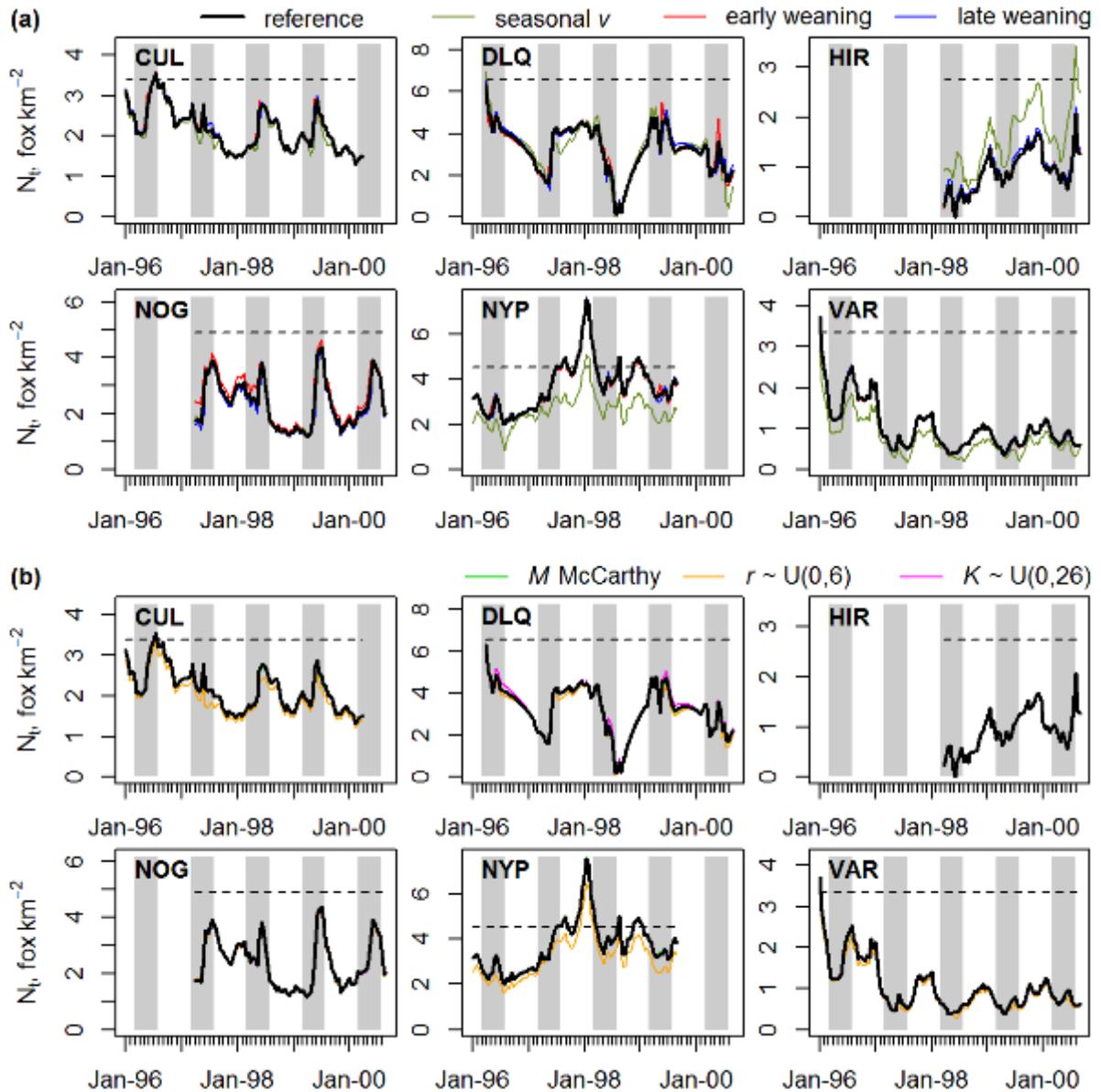


Figure 7.11. Sensitivity of posterior median fox density on six estates to a) structural and b) prior distribution assumptions. Reference case shown is from the informative prior model. The dashed lines show the posterior median carrying capacity for the reference case.

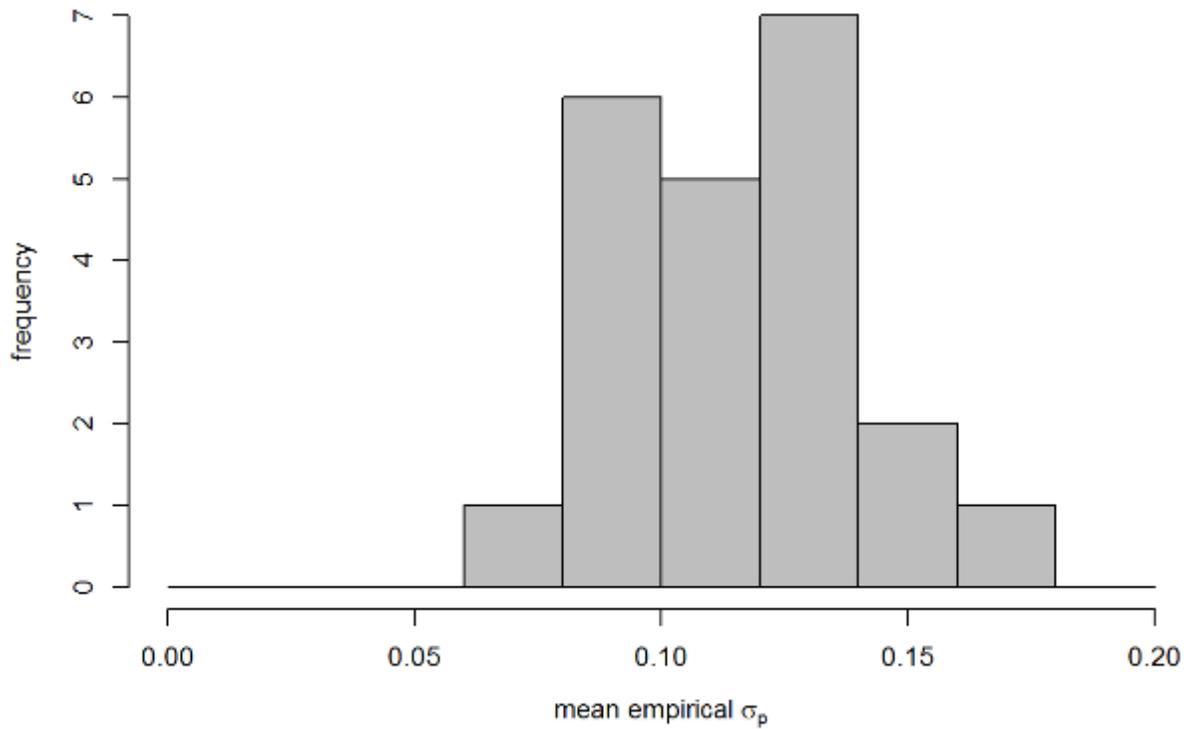


Figure 7.12. Histogram of the mean estimates of the empirical process error standard deviation from the 22 estates. These realised values were obtained by calculating the standard deviation in process errors across the time series for each MCMC chain iteration and summarising the mean of those. The fixed value used in the model was 0.2.

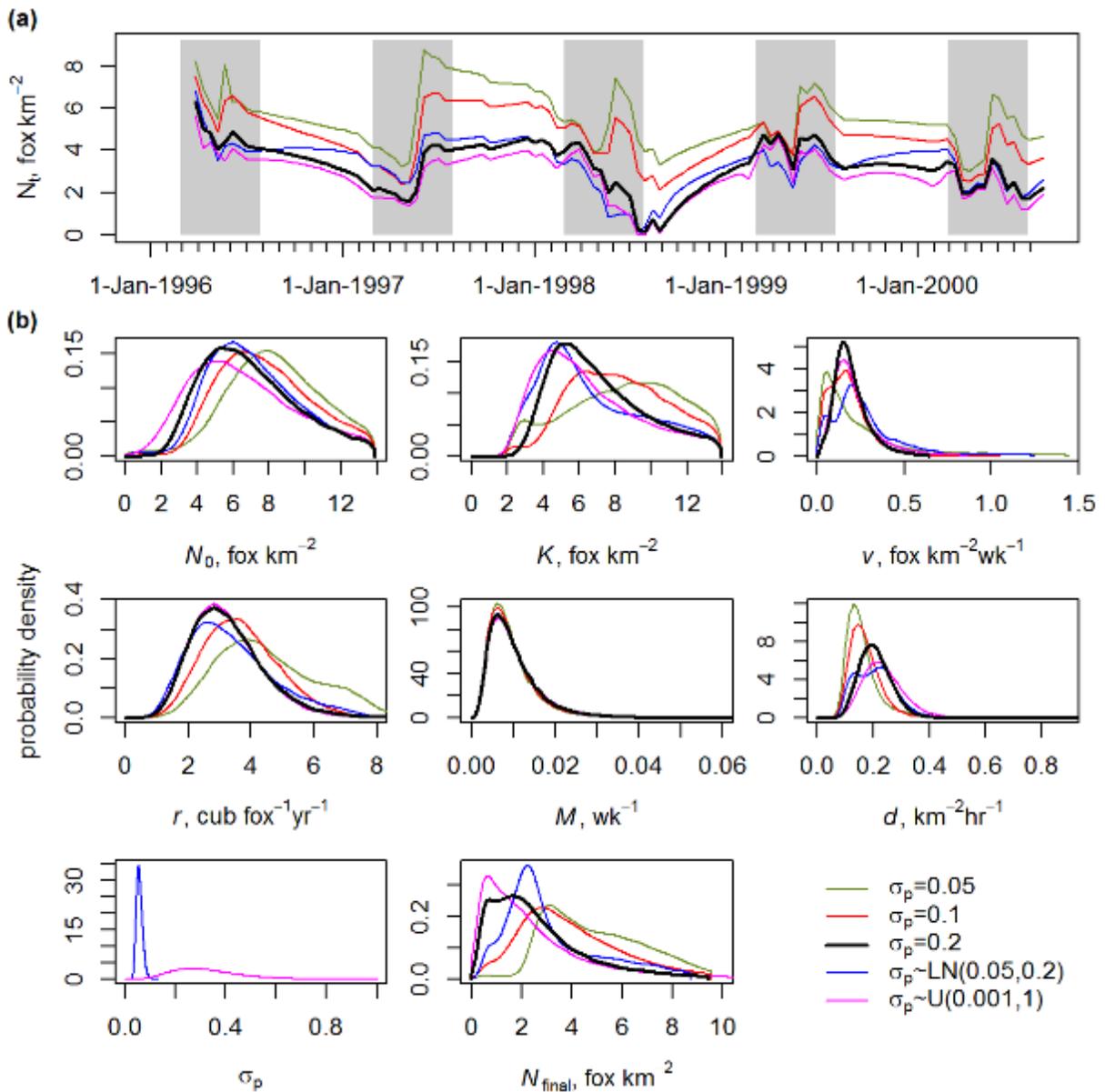


Figure 7.13. Results for DLQ showing sensitivity of a) posterior median fox density and b) marginal posterior parameter estimates to specification of the process error standard deviation, σ_p . The values of σ_p were either fixed at 0.05, 0.1, or 0.2, or were estimated using either a lognormal prior distribution with median of $\ln(0.05)$ and CV of 0.2 or a uniform prior with lower and upper bounds of 0.001 and 1.0, respectively. The reference case, where σ_p is fixed at 0.2, is shown in bold.

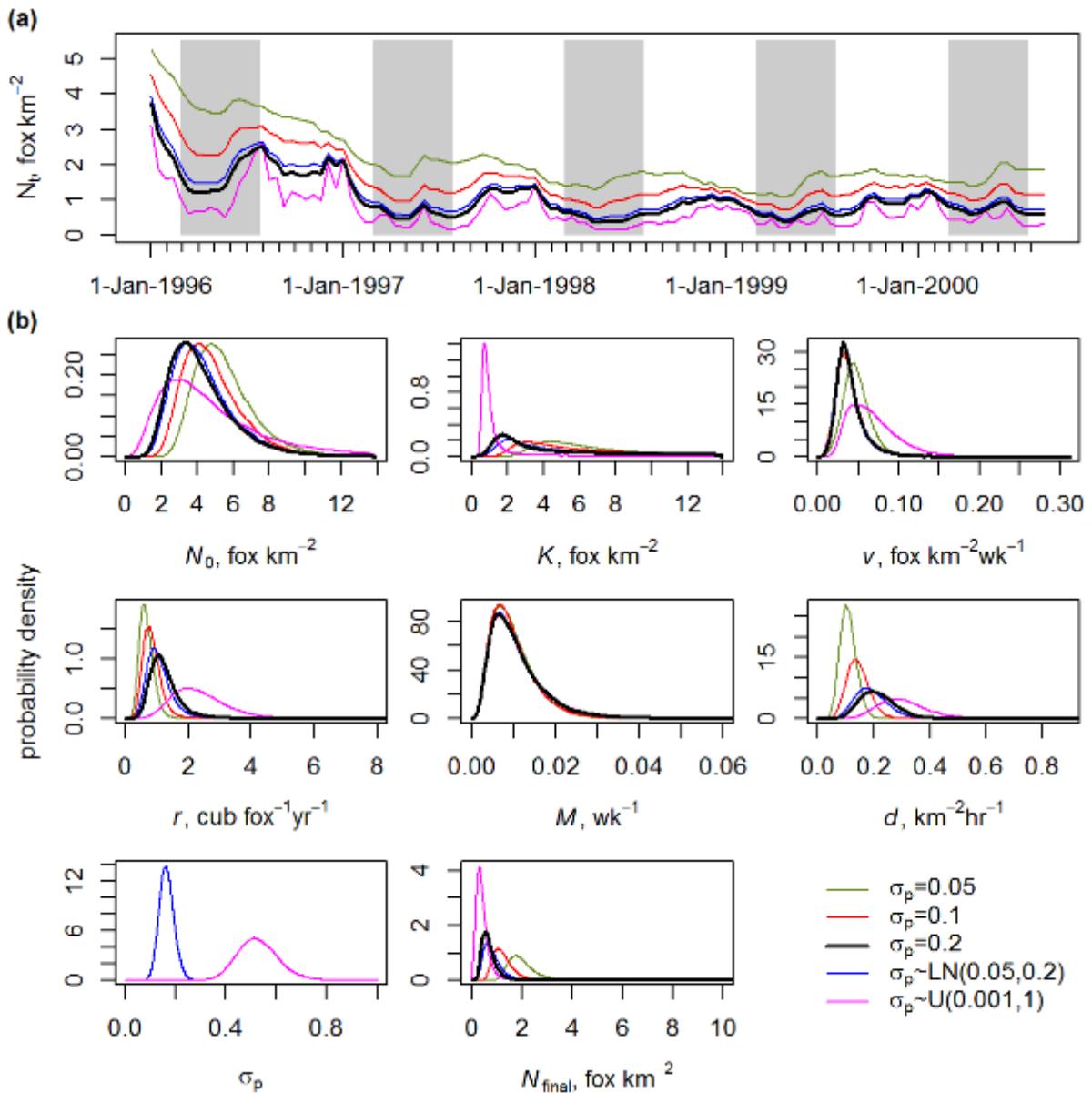


Figure 7.14. Results for VAR showing sensitivity of a) posterior median fox density and b) marginal posterior parameter estimates to specification of the process error standard deviation, σ_p . The values of σ_p were either fixed at 0.05, 0.1, or 0.2, or were estimated using either a lognormal prior distribution with median of 0.05 and CV of 0.2 or a uniform prior with lower and upper bounds of 0.001 and 1.0, respectively. The reference case, where σ_p is fixed at 0.2, is shown in bold.

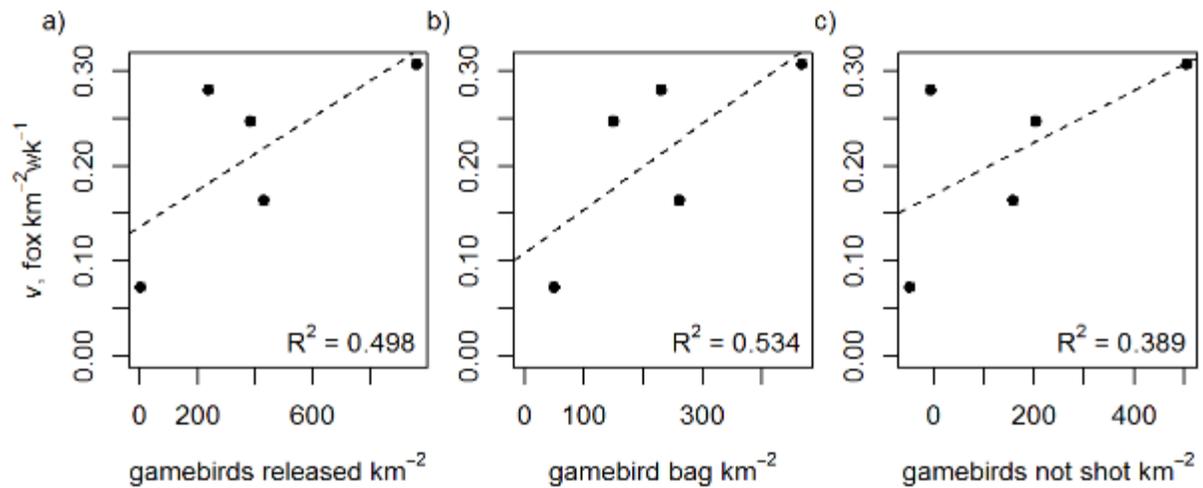


Figure 7.15. Relationships of fox immigration rate (v) with density of a) game birds released (pheasants and red-leg partridges), b) game birds shot, and c) game birds not shot from those released on five estates for which NGC data were available. Game bird bag and release data were obtained as mean values for years 1996-2000.

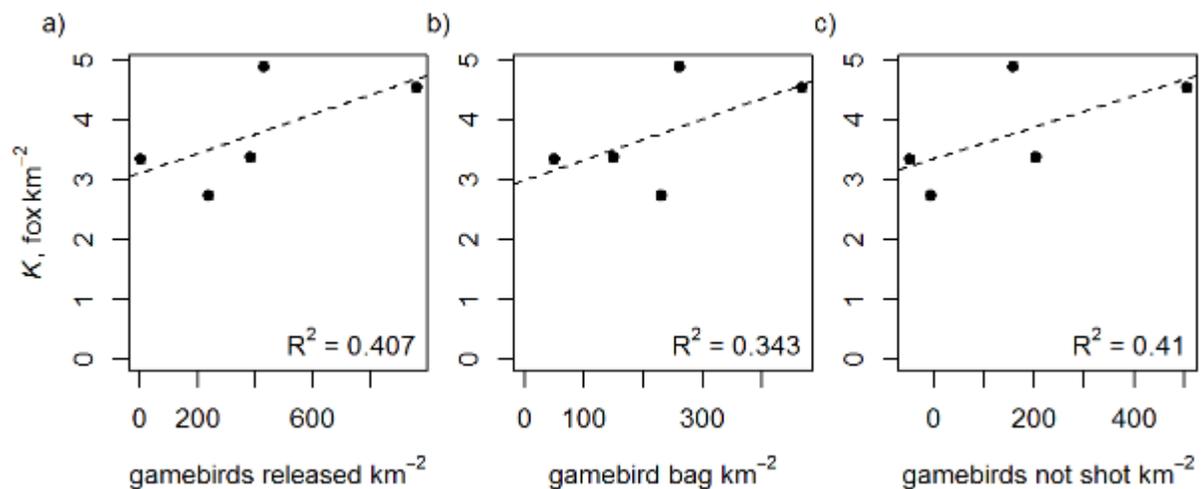


Figure 7.16. Relationships of fox carrying capacity (K) with density of a) gamebirds released (pheasants and red-leg partridges), b) gamebirds shot, and c) gamebirds not shot from those released on five estates for which NGC data were available. Game bird bag and release data were obtained as mean values for years 1996-2000.

Chapter 8: Evaluating alternative fox management strategies for the benefit of wild game

8.1 Introduction

Management strategy evaluation (MSE) was originally developed as an approach to whale harvest and fisheries management (Kirkwood 1997; Butterworth & Punt 1999; Sainsbury, Punt & Smith 2000). MSE applies computer simulations to evaluate a number of alternative management strategies using quantifiable performance measures derived from the management objectives (Smith, Sainsbury & Stevens 1999; Sainsbury, Punt & Smith 2000). MSE is used in evaluation of both adaptive and non-adaptive robust management strategies and has recently been proposed as a useful approach to solving terrestrial conservation and pest control issues where real-world experimentation is not feasible (Chee & Wintle 2010; Milner-Gulland *et al.* 2010; Bunnefeld, Hoshino & Milner-Gulland 2011). This chapter investigates use of the MSE approach to fox population control with a detailed case study on shooting estates in Britain.

Common approaches to the management of fish and wildlife resources and pest populations rely upon having methods for monitoring and estimating population size before and after a harvest or control action. These methods are subject to a wide range of uncertainties including sampling error, demographic stochasticity, environmental variability, lack of understanding of the dynamics of the system, and the imperfect implementation of management actions. MSE makes identification and modelling of uncertainties central to the approach, allowing the robustness of alternative management strategies in meeting objectives to be examined.

In the context of fox population control, the main components of a MSE model (Figure 8.1) include the operating model and the culling control model (McAllister *et al.* 1999). The operating model represents the ‘true’ state of the resource dynamics and interactions with control actions imposed by gamekeepers. The operating model incorporates a sub-model for the population dynamics, an observation sub-model to simulate

collection of ‘observed’ data, and an implementation sub-model to generate a cull that is used in the next time-step of the population dynamics model. The culling control model generates control rules that determine the control action to be taken within a management strategy, either through open- or closed-loop feedback control. In open-loop control, the control rule is predetermined and not influenced by the observed data simulated in the operating model, while in closed-loop feedback control the control rule is responsive to the observed data. For foxes, closed-loop feedback means that culling effort would be responsive to an indication of fox presence, as advised under the snaring Code of Practice (Defra 2005). Two alternative closed-loop culling control options can be adopted: a ‘model-free’ approach where the control rule is based directly on the observed data, or a ‘model-based’ approach where the control rule is based on model parameters estimated from the observed data using an assessment model (McAllister *et al.* 1999; Rademeyer, Plagányi & Butterworth 2007).

The models used in MSE can therefore capture several key uncertainties (Butterworth & Punt 1999). The population dynamics model captures both parameter uncertainty (i.e. lack of knowledge about the parameter values within a model structure) and process uncertainty (e.g. variation in the underlying demographic rate and processes that affect the population due to weather); the observation model captures observation uncertainty; and the implementation model captures the uncertainty related to how perfectly managers follow the culling control rules. In addition, structural uncertainty (i.e. lack of knowledge about how the system should be modelled) can be tested by evaluating structurally different versions of the operating model (McAllister *et al.* 1999; Milner-Gulland 2011).

If possible, the objectives against which the performance of a fox control strategy can be measured are usually based upon prey populations of economic or conservation importance rather than on the fox population itself. On British shooting estates, the control of foxes usually aims to benefit populations of game species, e.g. pheasant (*Phasianus colchicus*), red-legged partridge (*Alectoris rufa*) or grey partridge (*Perdix perdix*). Fox predation is a limiting factor for threatened grey partridge populations (Tapper, Potts & Brockless 1996), and though more abundant, many wild pheasant populations are also

unsustainable in presence of fox predation (Baker *et al.* 2006; Draycott *et al.* 2008). This leads a large number of estates to release hand-reared birds to supplement wild stocks so that a commercial harvest can be removed (Tapper 1992). Fox control in Britain also aims to benefit other threatened species – e.g. brown hare (*Lepus europaeus*), lapwing (*Vanellus vanellus*), stone curlew (*Burhinus oedicanus*) – that suffer from fox predation (Reynolds & Tapper 1995b; Fletcher *et al.* 2010).

Similar to the problems in estimating the size of fox populations, it is typically difficult to estimate prey population sizes, so performance measures are usually taken from prey monitoring data. For gamebirds, these performance measures include: 1) annual harvest (i.e. the gamebag), which can be monitored relatively easily from bag returns; 2) breeding productivity of wild birds, which requires both spring and autumn counts; 3) survival of released birds, which requires some level of tagging effort when wild birds are also present. All of these performance measures require the prey population dynamics to be modelled separately to foxes within an MSE. While this is possible, it adds additional uncertainties related to the prey population (about which little may be known) and also depends upon having knowledge of fox diet on an estate, the composition of which varies both seasonally and between regions (Heydon & Reynolds 2000a; Baker & Harris 2003; Webbon *et al.* 2006).

A performance measure without the requirement to model the prey population on an estate is the weekly food requirement of the fox population density. This has the advantage that it can be easily aggregated over periods of interest to the gamekeeper, e.g. the bird nesting period (1 March –31 July, hereafter referred to as nesting period). The fox control strategy that results in the lowest density of food required to satiate the fox population at different times of year is assumed to be the most effective strategy with respect to the objective of benefitting the prey population. In the absence of studies indicating the functional response of fox diet to game density, total food requirements are used as a proxy for the likely impact on game. Several studies have examined fox diet composition in Britain (Reynolds & Tapper 1995a; Baker & Harris 2003; Webbon *et al.* 2006) but none have examined the food requirements of British foxes. In any case, the proportion of a particular

prey species in a predator's diet does not indicate the importance of predation for the prey population, e.g., grey partridge may only comprise a small proportion of fox diet but the effect of fox predation on the population may be high (Reynolds & Tapper 1995a, 1996). Captive feeding trials using natural prey items have been used to estimate the food requirements of foxes in France (Stahl 1990) and North Dakota (Sargeant 1978), but only the North Dakota study provided a detailed temporal breakdown of the weekly food requirements of growing cubs and of male and female foxes. This detail is important as culling different components of the total population during the year could result in significantly different food requirements. Given assumed body weight of prey species, food requirements can be converted into a required density of certain prey species, which may be of particular interest for threatened prey populations, e.g. grey partridge, where only short periods of foxes feeding exclusively on such prey could be devastating.

The most effective control strategy is unlikely to be consistent between estates due to differing objectives and local fox population dynamics. Shooting estates can be broadly split into two extreme types: wild bird estates and released bird estates. Wild bird estates aim to achieve a harvestable surplus from wild stock during the shooting season and do not release birds, while released bird estates hand-rear birds in pens and release them into the wild a minimum of one month before the shooting season begins. The length of the shooting season varies for each game species, though for most species it is from the start of September until the start of February. Fox control objectives therefore depend on the type of estate as well as the game species for which the estate is managed. Wild bird gamekeepers usually put more effort into fox control and target most of their effort during the spring to boost breeding productivity. Released bird gamekeepers are less concerned with the productivity of gamebirds in the wild, and target most of their fox control effort during the autumn to increase survival of released birds that they must spend time rearing during the spring (Reynolds & Tapper 1996). It is important to recognise that these different gamebird production strategies imply different fox control strategies, with trade-offs related to the costs of gamebird releasing versus fox control.

The two extreme types of estate lead naturally to two alternate seasonal strategies to explore: control only during spring and summer (1 February – 31 July), typical of a wild bird gamekeeper; and control only during summer and autumn (1 June – 31 November), typical of a released bird gamekeeper. Two further alternate strategies can include control year-round but with seasonal variation as observed in the FMS lamping data (i.e. the same time series used to generate data in the simulation-evaluation testing in Chapter 3), to represent the ‘average’ gamekeeper; and control year-round with uniform effort. The effect of no control is determined under each of these four strategies where the effort levels are zero. To provide focus to the analysis, the current chapter develops a MSE analysis primarily for wild bird estates. This chapter thus aims to 1) use open-loop MSE and model-free closed-loop MSE on a subset of the FMS estates to determine which of these alternative strategies and culling methods best achieves the objective of low fox food requirements during the nesting period, and 2) examine the trade-offs between effectiveness and effort required to achieve a given degree of control under these culling strategies and feedback options.

8.2 Methods

8.2.1 Data

Simulation of fox population dynamics under alternative management strategies was performed using the population dynamics model specified in Chapter 3 as an operating model. The parameter values used were the estimates obtained from the joint posterior probability distributions from FMS estates in Chapter 7. Management decisions may be influenced by ecological conditions on an estate, e.g. effective management may require a different strategy where immigration rate is high than where it is low. This uncertainty can be examined using a range of operating models, termed the reference set (Rademeyer, Plagányi & Butterworth 2007), which represent the range of ecological conditions experienced by different shooting estates, i.e. those estates with the highest and lowest posterior estimates for each model parameter (Chapter 7). A subset of nine FMS estates was chosen (Table 8.2). The estates were also chosen to represent the full range in size within the FMS as this may also influence the management decisions. Sets of values were drawn from

the full joint posterior probability distribution for each simulation to ensure that the correlation structure of the estimates was preserved when simulating uncertainty in parameter values.

8.2.2 Operating model

8.2.2.1 Population dynamics model

As the MSE options applied in this chapter are not model-based there was no need to incorporate an assessment model. The time step of the operating model was therefore chosen to be one week rather than two weeks to make best use of the weekly food requirement data (Sargeant 1978) and to allow finer control of the culling options. The first week of the simulated population was assumed to begin at the start of September 2000 to follow on from the end of the FMS data, which ended on 31 August 2000. As the weekly food requirement of juvenile foxes evolves during their first year and those of male and female foxes also differ, to allow the food requirements on an estate to be simulated accurately the aggregate state-space model used previously to model the sightable fox population density on estates (N_t , see Chapters 3 & 7) was split into adult $N_{a,t}$ and juvenile $N_{j,t}$ components:

$$N_t = N_{a,t} + N_{j,t} \quad \text{Eq. 8.1}$$

A summary of all model parameter and variable symbols and definitions used in this chapter is provided in Table 8.1. Use of a stage-structured model to simulate population and culling dynamics introduced complications as the adult and juvenile fox population components may have different dynamics. For example, juvenile foxes are more likely to disperse (Macdonald & Voigt 1985) and are potentially more vulnerable to culling, meaning that most immigrant foxes are likely to be juveniles and that juvenile foxes are more likely to be culled first. A stage-structured model should ideally incorporate separate adult and juvenile parameters to account for these effects, but as discussed previously. Without any stage-structured data this would result in a model with poor parameter identifiability and so was not explored for parameter estimation (Chapter 3). To use parameter values estimated from an aggregate model, the mathematical subdivision of the model structure must be

performed carefully so that parameter definitions are consistent and the total fox population simulated by both models is the same.

Whilst using the same parameters as the aggregate model, the stage-structured model allowed incorporation of additional stage-specific realism that could be expected to affect the food requirements on an estate. Fox migration during the August to March period was assumed to be juvenile foxes only by incorporating Boolean indicator variables ($b_{a,t}$, $b_{j,t}$) that set weekly migration in or out of the adult population on an estate to zero between August and March, and migration in or out of the juvenile population to zero between April and July. To link the adult and juvenile components of the population together, the week containing the mean birth date of cubs (1 April) was chosen to be when any juvenile foxes remaining on an estate were recruited into the adult population. Adult and juvenile components of the total fox population were therefore defined as:

$$N_{a,t} = [\max\{N_{a,t-1}e^{-\tilde{M}} + b_{a,t-1}\tilde{v}(1 - N_{t-1}/\tilde{K}) - L_{a,t-1} - S_{a,t-1}, 0.001\}]e^{(\varepsilon_t - \sigma_p^2/2)} \quad \text{Eq. 8.2}$$

$$N_{j,t} = [N_{j,t-1}e^{-\tilde{M}} + b_{j,t-1}\tilde{v}(1 - N_{t-1}/\tilde{K}) + w_{t-1}\tilde{r}N_{t-1}(1 - N_{t-1}/\tilde{K}) - C_{t-1} - L_{j,t-1} - S_{j,t-1}]e^{(\varepsilon_t - \sigma_p^2/2)} \quad \text{Eq. 8.3}$$

where $L_{a,t}$ and $S_{a,t}$ are the adult lamping and snaring culls, respectively, $L_{j,t}$ and $S_{j,t}$ are the juvenile lamping and snaring culls, respectively, C_t is the cull of cubs at earths, and all other parameters and scalar variables are defined as previously (Chapter 3). All parameters that vary as random variables drawn from the joint posterior across simulations are denoted with a tilde (e.g., \tilde{v}). Fox density on an estate was simulated from 1 September 2000 until 31 December 2004, taking initial density \tilde{N}_0 as the final estimated density on each estate from Chapter 7.

Lognormal process error terms were assumed, where ε_t were randomly sampled as i.i.d. deviates from a standard normal distribution that has a standard deviation, σ_p :

$$\varepsilon_t \sim N(0, \sigma_p) \quad \text{Eq. 8.4}$$

The fixed value of σ_p used in the estimation model (0.2, Chapter 7) was based on a two-week time step. This value was converted for use on a weekly time step by recognising that lognormal distribution error variances are additive when the random error deviates are independent of each other, giving a scaled value for σ_p of 0.141 ($= \sqrt{0.2^2/2}$).

The juvenile fox population was assumed to be an aggregate male and female population until recruitment into the adult population as sex-structured cub growth data were not available. The juvenile:adult ratio used to initialise the model was obtained by running the operating model without culling at the posterior median values for the model parameters. The model was run for enough years that the equilibrium population was reached and the initial ratio was taken from the equilibrium population in the week containing 1 September. Juveniles were assumed to recruit with an equal sex ratio. The male and female components of the adult fox population were separated for calculation of sex-specific food requirements. This was achieved by assuming that adult male and adult female foxes were equally vulnerable to culling by lamping and snaring and performing the split at the end of each week after any cull had been removed using a constant male-to-female sex ratio, φ . It is common for dominant male/female pairs to tolerate related non-breeding ‘helper’ females (Macdonald 1979; Reynolds & Tapper 1995a), although helper females are less common in populations subject to high levels of culling mortality (Lloyd 1980). To simulate the presence of a small number of helper females on an estate, φ was fixed at 0.4, i.e. 1 male to 1.5 females. Male $N_{m,t}$ and female $N_{f,t}$ components of the adult fox population were defined as:

$$N_{m,t} = \varphi N_{a,t} \quad \text{Eq. 8.5}$$

$$N_{f,t} = (1 - \varphi) N_{a,t} \quad \text{Eq. 8.6}$$

Weekly cull data were simulated using the total lampable population density because as part of the lampable fox population, foxes were assumed to be active away from the earth, which meant they were also at risk of capture by snaring. The order by which the total

lamping cull L_t or total snaring cull S_t occurred in a given week was randomised by simulating a Bernoulli random variable h_t that took a value of zero if lamping occurred first, or a value of one if snaring occurred first. For the lamping cull, the number of foxes sighted Y_t was simulated from the fox density as a Poisson random variable given the number of hours of lamping E_t :

$$Y_t \sim Pois(\tilde{d}E_tN_t) \quad h_t = 0 \quad \text{Eq. 8.7}$$

$$Y_t \sim Pois(\tilde{d}E_t[N_t - S_t]) \quad h_t = 1$$

where d is the rate of successful search. The lamping effort level was set by the control action determined by the culling control model. The total density of foxes culled by lamping was then calculated as:

$$L_t = p_k Y_t / A \quad \text{Eq. 8.8}$$

where p_k is the probability of a sighted fox being killed and A is the estate area. The mean observed value of p_k from the FMS data was 0.30 but there was large variation around this value reflecting occasions when gamekeepers were unable to shoot any of the foxes sighted, and other nights when they shot all foxes sighted. The observed distribution of p_k was therefore U-shaped, with most of the values at either 0 or 1. To model variation in the probability of lamping success per week, values for p_k were randomly generated from a distribution based upon the beta-binomial. The beta-binomial distribution is a binomial distribution with parameters for the number of trials and probability of success, but whose probability of success is not a constant but it is generated from a beta distribution. This allows U-shaped distributions, but without modification the generated numbers range from zero to the number of trials. To constrain the generated numbers to the $[0, 1]$ interval required, it was necessary to divide them by the number of trials (set equal to 100 here). Numbers were generated using the ‘rbetabinom’ function from the R package ‘VGAM’ (Yee 2010) by using values of 0.3 and 0.75 for the ‘prob’ and ‘rho’ arguments, respectively.

The total density of foxes culled by snaring was simulated as:

$$S_t = \begin{cases} p_s(N_t - L_t) & h_t = 0 \\ p_s N_t & h_t = 1 \end{cases} \quad \text{Eq. 8.9}$$

where p_s is the probability of snaring success per fox per week. The value of p_s was dependent upon the number of snares set in each week (see 8.2.3.2). The snaring effort level was set by the control action which was determined by the culling control model.

The potentially higher vulnerability of juveniles to culling was accounted for by assuming that any cull removed from the total population in a given week would be taken first from the juvenile component until it was fully depleted, then from the adult component. The juvenile and adult laming culs were calculated from L_t as:

$$L_{j,t} = \begin{cases} L_t & N_{j,t} \geq L_t \\ N_{j,t} & N_{j,t} < L_t \end{cases} \quad \text{Eq. 8.10}$$

$$L_{a,t} = \begin{cases} 0 & N_{j,t} \geq L_t \\ L_t - L_{j,t} & N_{j,t} < L_t \end{cases} \quad \text{Eq. 8.11}$$

Following similar logic, the juvenile and adult snaring culs were calculated from S_t as:

$$S_{j,t} = \begin{cases} S_t & N_{j,t} > L_{j,t}; N_{j,t} - L_{j,t} \geq S_t \\ N_{j,t} - L_{j,t} & N_{j,t} > L_{j,t}; N_{j,t} - L_{j,t} < S_t \\ 0 & N_{j,t} = L_{j,t} \end{cases} \quad \text{Eq. 8.12}$$

$$S_{a,t} = \begin{cases} 0 & S_{j,t} = S_t \\ S_t - S_{j,t} & S_{j,t} < S_t \end{cases} \quad \text{Eq. 8.13}$$

The cull of cubs at breeding earths (C_t) was assumed to be removed immediately prior to recruitment of cubs into the juvenile component of the lampable fox population:

$$C_t = p_c w_t r N_t (1 - N_t/K) \quad \text{Eq. 8.14}$$

where p_c is the probability of a cub being killed at an earth, which was assumed to be constant over time. Data from 39 earths suggest that nearly all (88%) of cubs seen at earths are killed (Reynolds 2000). If the assumption is made that once an earth has been found all cubs are killed, e.g. by using terriers to bolt them above ground to waiting shotguns, this

probability will equal the probability of locating an earth on an estate. This probability was set by the control action determined by the culling control model.

When both components were summed using Eq. 8.1, the difference in weekly population density values between the aggregate and stage-structured model was <1% under a range of input parameters and culling strategies. This was deemed an acceptable approximation.

8.2.2.2 Observation model

The culling control rules in the open-loop MSE are predetermined and so control actions do not depend on observed data. However, for this closed-loop MSE, the observation model determines whether and/or how much culling effort is used in a given week, with the culling control rules only being actioned if the observed data are above a threshold value. Several types of data on a fox population can be observed using either direct (counts of foxes) or indirect (counts of their signs) methods (Wilson & Delahay 2001; Sadlier *et al.* 2004). Gamekeepers can perform some of these methods during the culling process or as part of their regular duties whilst walking around their estate, but others require more survey effort and/or expertise.

Lamping sighting rate is an index of abundance that can be obtained by gamekeepers during the culling process. It is possible for a gamekeeper to monitor this index and use it to determine how much control effort to use in subsequent weeks, i.e. if it is above a threshold. Sighting rate may also be used to estimate fox density from the cull given a rate of successful search estimate from previous modelling of data from the estate, and to directly determine control effort based upon fox density. However, as a culling-dependent index it is only available when lamping effort has been used. This is problematic if there is zero lamping effort, i.e. under a strategy where lamping is not a method used in a given week. Culling-independent indices include activity indices such as faecal or prey remains counts. These indices can be obtained throughout the year and bring the advantage that control effort can be used reactively, but come at the cost of additional survey effort to gather them. This effort can often be worked into performing other duties across an estate during the week. The

observation model used a faecal survey index F_t to determine the culling control rule in closed-loop simulations. This was achieved by simulating a scat (faecal) search process.

Scat surveys along linear features have been used previously to estimate absolute fox density at the landscape scale in Britain (Webbon, Baker & Harris 2004). Linear features are landscape components that are linear in nature, e.g., hedgerows, fences, stone walls, rivers, farm tracks, paths and main road verges. Webbon *et al.* (2004) surveyed 444 1-km squares distributed within each landscape type. Obtaining an adequate sample size of 1-km squares precludes estimation of absolute density at the estate scale using a similar scat survey. In addition, abundance estimates obtained by scat counts have also recently been questioned (Güthlin *et al.* 2012). Nevertheless, simulation of the number of new fox scats found per week during a search can be used as an indicator of fox presence to determine whether culling effort is used in a given week, i.e. if the number of fox scats found is > 0 . The number of scats found will depend upon the fox density simulated each week by the population dynamics model and a length of linear feature surveyed on an estate dependent upon the level of search effort per week.

Gamekeepers were assumed to conduct the scat search on the first day of the week, i.e. prior to any use of culling effort. Incorporation of variable search effort was achieved by calculating the length of linear feature walked by a gamekeeper each week Q_w :

$$Q_w = TV \quad \text{Eq. 8.15}$$

where T is the number of search hours per week and V is the walking speed. On flat terrain, average human walking speed is 1.4 m/s (5.0 km/h; Tobler 1993; Levine & Norenzayan 1999; Mohler *et al.* 2007). However, a gamekeeper searching for scats in the linear features of an estate is likely to be travelling slower than the average person. Tobler (1993) suggests that off-path travel is at 60% of average speed, but the linear features usually travelled along do not seriously impede walking speed. Processing of visual information has been shown to reduce walking speed, and under higher rates of visual flow the average walking speed was reduced to 1.21 m/s (4.36 km/h; Mohler *et al.* 2007). This seemed a reasonable reduction in

average speed for a gamekeeper who would need to search the area in front of them and was therefore the speed assumed to equal V in these simulations.

The total length of linear feature on each estate was unknown. Instead, estimates of the length of linear feature per square-kilometre within different Environmental Zones within Britain were used (Jongman & Bunce 2009). Environmental Zones are an alternative aggregation of similar land classes to that used in Chapter 4 but the six zones broadly represent arable, pastoral and upland habitats; three in England and Wales, and three in Scotland (Haines-Young *et al.* 2003). The environmental zone in which each estate was located was determined using a GIS, and the estimated length of linear feature on each estate Q_A was calculated as:

$$Q_A = Q_L A \quad \text{Eq. 8.16}$$

where Q_L is the estimate of linear feature per square-kilometre in the Environmental Zone the estate is located within, and A is the estate area. These values are shown in Table 8.3.

Webbon *et al.* (2004) estimated that mean fox defecation rate of British foxes was 8 scats fox⁻¹ day⁻¹ (95% CI, 6.73-8.59). Variation in defecation rate was simulated by assuming this estimate was normally distributed and drawing a random number from this distribution. The same 95% confidence interval was obtained using a mean of 7.66 and standard deviation of 0.475 scats fox⁻¹ day⁻¹. The simulated value was multiplied by seven to convert it to a weekly defecation rate R . Webbon *et al.* (2004) used bait-marking trials to estimate that the mean proportion of scats that were deposited in linear features was 0.057 (95% CI, 0.034, 0.078). Variation in the proportion of scats deposited in linear features P_L was simulated by assuming that this estimate was normally distributed and drawing a random number from this distribution. The same 95% confidence interval was obtained using a mean of 0.0565 and standard deviation of 0.0112.

The total number of scats present in the length of linear features per week F_L was calculated by the equation:

$$F_L = (NQ_W R_W P_L) / Q_A \quad \text{Eq. 8.17}$$

where N is fox density. The simplest assumption would be that all scats in linear features walked by a gamekeeper would be detected, but this is highly unlikely to be true. Instead, error in the number of scats found was incorporated into the simulation using a parameter for the probability of a present scat being detected P_F and by assuming that the number of scats found per week F_t was a Poisson random variable:

$$F_t \sim \text{Pois}(F_L P_F) \quad \text{Eq. 8.18}$$

There was no available information on what value P_F might take. The effect of different values of P_F was examined using values of 0.5 and 0.8 to represent medium and high probability of detection, respectively. The effect of the number of search hours per week was examined using 2, 4 and 8 hours per week, with the highest value reflecting a full working day. It was assumed that all scats located each week were marked in some way so that gamekeepers would be able to distinguish fresh scat (<2 weeks old) from older scat. The search effort was also assumed to be separate to other estate activities conducted by the gamekeeper and so represents the maximum extra cost.

The observation model also used a culling-dependent index as when lamping was a method used within a culling strategy, an index of sighted foxes that were not killed U_t was obtained. This was a binary index that determined whether culling took place in a given week depending upon whether any sighted foxes were not killed in the previous week. If any foxes were missed, it was assumed they would remain resident on the estate. Thus if the value of U_t was equal to one, culling was implemented and scat search effort was not used in that week. U_t was calculated using the simulated value of p_k in each week:

$$U_t = \begin{cases} 0 & Y_{t-1} = 0 \\ 0 & Y_{t-1} > 0; p_k = 1 \\ 1 & Y_{t-1} > 0; p_k < 1 \end{cases} \quad \text{Eq. 8.19}$$

8.2.3 Culling control model

Four strategies with different timing of control were examined: 1) year-round control with uniform effort, 2) year-round control with seasonal variation in lamping effort, 3) spring-summer control between February and July (referred to hereafter as ‘spring-only’ control), and 4) summer-autumn control between June and November (referred to hereafter as ‘autumn-only’ control). As detailed in Chapter 2, gamekeepers at the time of the FMS used several methods: lamping, snaring, and destruction of cubs at earths using terriers, firearms, or (illegally) fumigants. Evaluation of alternative management strategies is therefore not simply an issue of timing of control, but also which method and what level of effort to use for each, e.g. different number of hours’ lamping or number of snares set or time spent searching for cubbing earths. Evaluation of variable effort actions means the relative effectiveness of different control methods can also be examined. This is of particular current interest in Britain because the use of terriers at cubbing earths has been outlawed since the time of the FMS by the Hunting Act 2004 (www.hmso.gov.uk), and the use of snares is controversial on account of poor target selectivity and injuries caused to captured animals (IWGS 2005; Short *et al.* 2012). The ability to determine how the effectiveness of fox control is impacted by the withdrawal of these methods could usefully inform policy debate.

To allow a meaningful comparison between the management strategies, effort levels must be standardised. This was achieved using fixed levels of annual effort for each method and allocating this effort according to each strategy. For example, the average numbers of hours’ lamping per week during the six-month control period in strategies 3 and 4 were twice that of the average weekly lamping effort in strategies 1 and 2, which are based upon year-round control. Gamekeeper lamping effort typically follows a pattern (Chapter 2); they go out for a couple of hours once or twice a week, and are finished and home before midnight. There is therefore a limit to the number of hours per night and number of nights per week they are willing or able to go out lamping. Likewise, as each snare must be checked at least once daily there is a workable maximum number of snares a gamekeeper can responsibly set while adhering to the snaring Code of Practice (Defra 2005). While there is no written

maximum, evaluating levels of snaring effort that do not represent good practice does not seem responsible.

The culling control model therefore contains rules for lamping, snaring and cub control and is used to define the control actions applied under each culling strategy each week. Under open-loop MSE, the control actions were applied naively without any feedback during the time periods dictated by each strategy. Under closed-loop MSE, the control actions were dependent upon the values of U_t and F_t . If either of these values were > 0 , culling would take place in that week at the effort levels determined by the culling control model. If both values were equal to zero then no culling would occur that week. The implementation model was coupled with the culling control model, i.e. gamekeepers were assumed to follow the culling control rules perfectly. There are an infinite number of effort levels that could be chosen for each method, but the choice of the effort levels to evaluate for each method must take into account what is realistically achievable by gamekeepers. The effort levels used for each method are detailed below.

8.2.3.1 Lamping effort

Simulation of the fox cull under different levels of lamping effort was achieved by using different values for the annual number of lamping hours. Under each strategy, this number is translated into a weekly number of lamping hours applied in Eq. 3.8. The expectation is that more effort results in higher numbers of fox sightings and therefore more foxes culled by lamping each week. Across all estates in the FMS, the maximum annual number of lamping hours was on VAR and was 537 hr yr^{-1} . This was assumed to represent the upper limit of what is achievable by any gamekeeper. To evaluate a range of lamping efforts, 0%, 25%, 50%, 75% and 100% of this maximum number were used as effort levels. For strategy 2 (year-round control with seasonal variation in lamping effort) the same approach was used as in Chapter 3: i.e. the number of hours of lamping in each week was obtained by scaling the implied weekly effort by the proportional effort in each week of the year observed in the FMS data. This gave realistic seasonal variation in lamping effort, with less effort in summer and mid-winter and more effort in the spring and post-harvest (Fig. 2.3a).

8.2.3.2 Snaring effort

Simulation of the fox cull from snaring in Chapter 3 used a probability of snaring success per fox per week p_s that was set at a constant value of 0.05. This was not based upon a number of snares set. To evaluate different snaring levels it was necessary to simulate the cull from snaring given a variable number of snare nights (one snare set for one night), meaning that p_s was required to vary with the number of snare nights used in a week s_t . As the number of snares in use increases, it can be assumed that the probability of any snare catching a fox will eventually become one, provided a fox is present to be caught. This meant that the function used to calculate p_s based upon the number of snare nights must be monotonically non-decreasing. This was achieved by using the cumulative distribution function (cdf) of the geometric distribution (a special case of the negative binomial distribution where the number of successes, i.e. fox captures, equals one). The geometric distribution is used to model the number of failures until success occurs and was used here to model the probability of snaring success per fox given there are $s_t - 1$ failures until one success occurs, i.e. that one fox is captured using s_t snare nights per week or less. The probability of success in this distribution was assumed to equal 0.00175, which was the probability of fox capture per snare per day f . The analysis used to estimate f is detailed in Appendix G.

The snaring effort levels used were based upon snaring effort data from 33 gamekeepers that were involved in a trial of different snare types (Short *et al.* 2012). The maximum number of snares nights used per year was $1992 \text{ km}^{-2} \text{ yr}^{-1}$. To evaluate a range of snaring efforts, 0%, 25%, 50%, 75% and 100% of this maximum number were used as effort levels. These snare densities were used to calculate s_t on each estate. 391 snares was the maximum number of snares used per night (on a 10 km^2 estate). This level of snaring effort was used for less than one month and was not considered to be sustainable for an entire year under the snaring Code of Practice (Defra 2005). The expected value of p_s given each snaring effort level was therefore obtained from the geometric cdf (Figure 8.2).

8.2.3.3 Cub removal

No information was available within the FMS on the proportion of cubs that were killed at earths or the proportion of fox earths within an estate that were found. There were also no data available from the FMS on the effort used to find earths and kill cubs on different estates. It was therefore necessary to assume that greater effort to remove cubs would be reflected in an increased probability of finding breeding earths and therefore an increased probability of a cub being killed at the earth. To evaluate a range of efforts and the importance of removing cubs at breeding earths before they recruit into the lampable population, the levels of p_c used in Eq. 8.14 were set at 0, 0.2, 0.5 and 0.8. The removal of 100% of cubs was not considered. Because fox territories do not match estate boundaries, some earths from which cubs may recruit into the within-estate population may be located beyond the estate boundary. These cubs would therefore not be subject to control effort directed at earths on the estate. Also, once earths are disturbed vixens may move the cubs to a different location that may be up to 1.5 km away (Lloyd 1980; Reynolds, Goddard & Brockless 1993). This further reduces the probability that all cubs in the modelled population would be killed.

8.2.4 Food requirements

Mean food consumption rates of 0.48 kg/kg adult/week were recorded from male and female foxes in North Dakota weighing 4.75 kg and 4.68 kg, respectively (Sargeant 1978). British foxes are on average larger and heavier than those in North America, at 6.5 kg for males and 5.5 kg for females (Reynolds & Tapper 1995b), so these food requirements were scaled and raised to the power of 0.75 to account for metabolic rate (Kleiber 1932). Male and female adult fox mass specific consumption rates in Britain were calculated as 0.44 and 0.46 kg prey/kg adult/week, respectively. The first teeth in cubs do not begin to erupt until late in the third week of age (Linhart 1968; Sargeant 1978; Lloyd 1980), so it is assumed that cubs fed exclusively on milk during their first four weeks as weaning could not begin until after milk teeth had erupted. During this four-week period food consumption rate of females with young increased on average by 0.57 kg prey/cub/week which was attributed to the additional prey requirement necessary for lactation (Sargeant 1978). Scaled for British fox

body weight, the lactation period prey requirement was calculated as 0.64 kg prey/cub/week. This meant that the annual food requirements for male and female adult foxes in Britain were therefore 150 and 132 kg, respectively.

Mean cub weight data obtained weekly during the first six months postpartum (Sargeant 1978) were fitted to a Richards' growth function using least squares (following Johnson, Sargeant & Allen 1975) that resulted in cubs reaching a mean adult weight of 4.72 kg at 12 months of age. Scaling this growth curve to the mean adult weight of British foxes (6 kg) allowed calculation of the weekly weight of cubs during their juvenile year. Weekly food consumption rates of cubs during their first six months (Sargeant 1978) were fitted using a Hassell (1975) function under the assumption that food consumption per cub peaked at 1.3 times mean adult levels at 28 weeks postpartum, declining to mean adult levels by 12 months of age when they reached mean adult weight (following Reynolds & Tapper 1995b). Finally, the fitted consumption/time curve was used to calculate the weekly cub food requirements. Addition of the female lactation period food requirement per cub over the first four weeks to the weekly cub food requirement, and removing it from the adult requirement gave the food requirement curves in Figure 8.3. Using this curve, each cub in Britain is assumed to consume 143 kg of prey during their juvenile year. This value is comparable with Baker & Harris (2003), who used similar calculations without giving weekly detail to report an annual cub prey requirement of 143 kg.

The operating model only monitored cubs as they recruited to the lampable juvenile population in each week following the weaned cub distribution. To account for food requirements of the cubs prior to this stage it was necessary to back-calculate the number of cubs recruiting in each week to give the number of cubs born eight weeks earlier, making the same assumption used previously that there was no within-estate non-culling mortality. Given these numbers the food requirement of the pre-recruitment cub population in each week was calculated using the cub food requirement growth curve in in Figure 8.3.

The weekly food requirement of the total fox population on each estate under each strategy and set of culling effort levels was simulated by drawing 1,000 sets of parameter values from the joint posterior probability distribution obtained in Chapter 7. All analysis

was performed within the R statistical software (R Core Team 2013). Results were summarised using the mean weekly food requirement across simulations. To evaluate the results with respect to the aim of control, these weekly values were summed over the nesting period to give the nesting period food requirement. This was used as an indication of the predation pressure on prey populations during this time.

8.2.5 Validation of the culling control model

To determine that the culling processes were correctly captured by the culling control model, reconstructed and projected nesting period food requirements were compared for DLQ. This estate was chosen as data on snaring effort were available from a previous survey recorded by the same gamekeeper in 1993 (Gamekeeper Methods Survey, unpubl. GWCT data). Lamping effort data were known from the Fox Monitoring Scheme. Cub removal rate was inferred based upon the observed number of cubs killed at earths and the reconstructed fox population density (Chapter 7), with a value of 20% giving the average observed number of cubs killed. In an average year on DLQ, there was 40 hours lamping used between February and May and 830 snare nights per km² used between May and August. Reconstructed food requirements on DLQ were obtained from the operating model using the observed cull of each method. The projected food requirements were obtained using the average annual effort and timing as inputs to the culling control model. This allowed the mean projected food requirement during the nesting period to be compared to the reconstructed food requirement during this period.

8.2.6 Operating model reference set

There were nine estates within the operating model reference set to examine the sensitivity of the results to the range of ecological conditions experienced on different estates. The reference set used in open-loop MSE also included alternative operating models related to different assumptions. First, in addition to the operating model where the standard deviation in process errors was assumed to be the same as in the estimation model (equal to 0.2 on a two-weekly time-step), two alternative operating models were used where σ_p was equal to 0.05 and 0.3 to examine the sensitivity to lower or higher process error. Secondly,

an alternative operating model was used that assumed that immigration was a seasonal process occurring only during the fox dispersal period of August to March, rather than a constant process year-round process. Thirdly, alternative operating models where carrying capacity of an estate was higher or lower relative to the estimated value from the posterior were used to examine the effect of increasing or decreasing the food supply, e.g. by releasing more or less game birds. This was achieved by multiplying K within each simulation by either 2.0 or 0.5. Lastly, alternative operating models where immigration was reduced or prevented were used to examine the effect of addressing source populations, e.g. through increased levels of fox control on neighbouring estates. This was achieved by multiplying v within each simulation by 0.5 or zero.

Sensitivity of the results to operating models that made alternative structural assumptions about the observation errors in fox sightings was not examined because the analyses in Chapter 7 suggested that the estimations were not sensitive to the choice of likelihood function (Poisson, negative binomial, or lognormal) used to model the sighting data when σ_p was fixed.

8.3 Results

8.3.1 Reconstruction vs. projection

The annual mean food requirements of the fox population during successive nesting periods on DLQ, reconstructed using the observed cull numbers, were 198 kg km⁻² (1997), 65 kg km⁻² (1998), 177 kg km⁻² (1999), and 160 kg km⁻² (2000). These results gave an across-year mean of 150 kg food required per km² during the nesting period. Using the operating model to project the population over a four-year period under best knowledge of observed culling effort levels resulted in 159, 154, 162 and 163 kg km⁻², or an across-year mean of 160 kg km⁻². The differences in annual values were due to the cull numbers simulated in the projection being averages across variable culling effort and success between simulations, causing them to be similar in each year, while the cull numbers used in the reconstruction were fixed observations. Within each year, the reconstructed mean weekly food requirements fell within the 95% credible interval of the projected food requirements.

The minimal difference between reconstructed and projected mean food requirements under similar culling efforts suggests that the culling control model is adequately capturing the culling process.

8.3.2 Open-loop MSE

On all estates the spring-only (February-July) control strategy resulted in the lowest mean food requirement of the fox population during the nesting period and was therefore expected to be the most effective with respect to wild gamebird production. Closer examination of the open-loop results on DLQ (Figure 8.4) shows that the mean nesting period food requirement using maximum levels of culling effort under this strategy was 23.25 kg km^{-2} , compared to $302.75 \text{ kg km}^{-2}$ when there was no control. The next most effective strategy with respect to wild gamebird production was year-round control with uniform effort, which under maximum levels of effort resulted in a 36.5 kg km^{-2} food requirement during the nesting period. Although the difference is less than 14 kg km^{-2} , this represents a 57% higher food requirement. The strategy of year-round control with seasonal lamping effort was slightly less effective than uniform effort, with 39.25 kg km^{-2} food required, because proportionally less lamping effort is used during the nesting period under this strategy (Figure 8.4). The least effective strategy with respect to wild gamebird production was the autumn-only (June-November) control, under which the fox population required 144 kg km^{-2} of food during the nesting period. While this represents a suppression of the fox population of over 50% relative to no control being performed, despite the use of the same maximal annual amount of culling effort this food requirement is 620% higher than it was under the most effective strategy.

The ranking of strategies was the same on each estate, meaning that strategy choice was not affected by the values of estimated parameters. However, the relative importance of different culling methods within each strategy was estate-dependent (Figure 8.5 - Figure 8.7, Figure H.1 - Figure H.6). Snaring and lamping differed markedly in their effectiveness on each estate, although cub removal was the least effective method on all estates as the difference in food requirements between 0% and 80% cub removal when there was no

snaring or lamping effort was small. On DLQ, there was little difference in the effectiveness of snaring and lamping in reducing the food requirement, as each successive level of snaring and lamping reduced the food requirement by a relatively similar amount (Figure 8.5). The most common result given these effort levels was that snaring was more effective than lamping. On VAR, near-minimum food requirements were achieved with only 25% of maximum snaring effort, while maximum lamping effort failed to achieve this degree of control (Figure 8.6). Only on one estate (OCS) was lamping was more effective than snaring, with the maximum level of snaring effort only achieving the same effect on food requirements as the 25% of maximum level of lamping (Figure 8.7).

The food requirements on each estate reflect the fox density. Under no culling effort, the requirement on VAR was only about one-third of that on DLQ and OCS (Figure 8.5 - Figure 8.7) because fox density was lower on this estate (cf. Chapter 7). The ability to reduce the food requirements to near-zero levels under high levels of effort appeared to depend upon the parameter values, in particular immigration rate. On OCS and VAR, which had very different food requirements under no culling effort, it was possible to reduce the requirement during the nesting period to 9 kg km^{-2} and 2 kg km^{-2} , respectively. This was because low fox density could be maintained on these estates due to v being low. In contrast, where v was higher on DLQ, it was only possible to reduce the food requirement during the nesting period to 18 kg km^{-2} .

Although the nesting period food requirements were lowest under spring-only control, the food requirements during the rest of the year were highest under this strategy as there was no control over-winter to remove immigrants (Figure 8.4). This exposed the trade-off between effective nesting period control and over-winter food requirement. Examination of this trade-off on DLQ for each combination of culling methods confirms that using all methods together under the maximum levels of effort is the most effective option at reducing nesting period food requirements (Figure 8.8). Removal of cubs at earths was the least effective option, even at the maximum 80% rate, as on its own this method was only able to reduce the food requirement during the nesting period to around 250 kg km^{-2} regardless of the control strategy. Lamping and snaring were therefore the most important methods.

Under maximum levels of effort for both on DLQ, lamping appeared to be slightly more effective compared to snaring when either method was used on its own.

Different trade-offs existed between the nesting period food requirement and the number of foxes killed annually to achieve that degree of population control under each strategy (Figure 8.9). Spring-only control was the most effective strategy in terms of nesting period food requirement, but was also the most efficient in terms of the number of foxes that needed to be culled annually to achieve this degree of control. The slight improvement in effectiveness of lamping at reducing the food requirement comes at a higher cost in terms of the number of foxes killed annually, which under the spring-only strategy was a difference of over two fox km⁻². The same pattern of spring-only control giving the lowest food requirement for fewest foxes killed is seen on other estates, although the most effective method varies between estates (Figure I.1 & Figure I.2).

The ranking of strategies on DLQ was not sensitive to the process error standard deviation, the only effect being that the food requirement under the autumn-only strategy and maximum effort levels became lower as σ_p increased (Figure 8.10). The assumption that immigration was a year-round or seasonal process did not affect the ranking but food requirements were lower under seasonal immigration compared to year-round immigration for all strategies (Figure 8.10). The scale of carrying capacity did not affect the strategy ranking, as lower or higher values for K only decreased or increased the food requirement, respectively (Figure 8.10). Reduction of immigration rate lowered the food requirements under all strategies and did not affect the ranking (Figure 8.10). When ν was zero, the food requirements were also zero under maximum effort levels. The sensitivity of results on DLQ was similar to that found on other estates (Figure J.1 & Figure J.2).

8.3.3 Closed-loop MSE

Compared to open-loop MSE, incorporation of feedback from the scat search within closed-loop MSE gave results which, though similar, were not quite as effective at reducing the food requirement of the fox population during the nesting period on DLQ (Figure 8.11). The ranking of strategies under maximum effort levels was the same as under open-loop

MSE, with spring-only control the most effective. Search time and probability of scat detection both affected the level of fox control predictably, with eight hours of searching per week and a high probability of detecting scat being the most effective combination. For all strategies, the open-loop option achieved the lowest food requirement during both the nesting period and the rest of the year relative to all closed-loop options (Figure 8.11). The trade-off between breeding success and over-winter survival of prey populations was therefore reduced by the naïve use of culling effort where feedback was not incorporated.

Relationships between the nesting period food requirements under maximum effort levels and the number of foxes killed annually to achieve this level of effectiveness were more complicated. On DLQ under a spring-only strategy, the open-loop option required the fewest number of foxes to be killed to achieve the most effective degree of control compared to closed-loop options (Figure 8.12). However, the results were different using other strategies as the open-loop option had the highest cost in terms of foxes killed annually to achieve the most effective control when compared to closed-loop options. The trade-offs under spring-only control differed between estates, although the spring-only strategy was the most efficient under all closed-loop options (Figure K.1 & Figure K.2).

Difference in the nesting period food requirement between open-loop MSE and the most effective closed-loop option (eight hours searching per week and high probability of detecting scat) under a spring-only strategy on DLQ was less than 5 kg km^{-2} . Culling in response to detection of scat can therefore achieve control that is almost as effective as culling without feedback, but at lower culling effort costs. This trade-off must be analysed in relation to the aims of fox control on an estate and whether the cost of 5 kg km^{-2} of food is too large. Comparing the most effective closed-loop and open-loop options under spring-only control, the closed-loop option required >2000 fewer snares nights per year (Figure 8.13) and >150 fewer lamping hours per year (Figure 8.14). These effort-savings are also seen in the year-round strategies, but are not quite as large. Naïve use of culling effort does not have any search time cost, whereas closed-loop options that incorporate feedback do have search time costs (Figure 8.15). Year-round strategies have higher search time costs than spring- or autumn-only control as there are more weeks' in which search time may be

required. For spring-only control, the search time cost is less than the saved number of hours of lamping effort when eight hours search time was available. This was not the situation for year-round control strategies. Savings in culling effort when feedback is incorporated must therefore be balanced with the search time cost.

8.4 Discussion

8.4.1 Strategy choice

This Chapter used management strategy evaluation to determine the most effective of four fox control strategies at reducing the nesting period food requirement on different shooting estates in Britain. MSE and related approaches have been used previously to evaluate alternative control strategies and methods for predator or overabundant wildlife species (red deer *Cervus elaphus*, Trenkel 2001; western grey kangaroo *Macropus fuliginosus*, Chee & Wintle 2010; racoon *Procyon lotor*, Martin *et al.* 2010), but this represents the first application of MSE to evaluate strategies to control fox populations on restricted-areas. The spring-only strategy where all available control effort was applied between February and July achieved the lowest nesting period food requirement. The greatest increase to wild bird productivity is therefore likely to be achieved using this strategy. Year-round control was the next most effective strategy, with autumn-only control between June and November being the least effective by a considerable margin. This ranking of strategies was consistent between open- and closed-loop MSE and across estates that experienced very different ecological conditions, as implied by the parameter estimates driving the simulations. These results were expected as the culling effort under the spring-only strategy was concentrated into a period incorporating the nesting period, meaning that the control exerted on the fox population during the nesting period was higher than under other control strategies.

Application of year-round control led to nesting period food requirements that were closest to the spring-only strategy but were on average across estates and effort levels about 48% higher. The strategy of year-round control with seasonal lamping effort resulted in slightly higher food requirements than when lamping effort was uniform in each week. This

was because proportionally less lamping effort was used during the nesting period under the variable lamping effort strategy, as gamekeepers in the FMS followed the previously observed pattern of increasing lamping effort during the post-harvest period when vegetation becomes lower and nights become longer (Reynolds & Tapper 1996). The differences in food requirements between the year-round and spring-only strategies translated to up to 60 kg km⁻² over the duration of the nesting period on some estates. This difference is of sufficient magnitude that it could plausibly affect the viability of wild bird populations.

Taking DLQ under maximum effort levels as an example, across this 3.2 km² estate the difference between spring-only control and the next best strategy (year-round uniform) was 43 kg of food during the nesting period, while the difference between the spring- and autumn-only strategies was 387 kg of food. While 43 kg does not appear large, it was equivalent to 29 rabbits (*Oryctolagus cuniculus*), 15 hares, 113 grey partridge, 86 red-legged partridge, or 33 pheasant on this estate [assuming average weights of rabbits 1.5 kg, hares 2.8 kg, grey partridge 0.38 kg, red-legged partridge 0.5 kg, and pheasant 1.28 kg; (Reynolds & Tapper 1995a)]. Predation of nesting gamebirds is often high relative to their abundance. Many wild pheasant populations are possibly unsustainable in the presence of fox predation during the nesting period (Baker *et al.* 2006; Draycott *et al.* 2008); and up to 60% of nesting grey partridge hens may be predated (Potts 1980), limiting production and subsequent breeding density (Tapper, Potts & Brockless 1996).

Rare species can be particularly vulnerable to the effects of fox predation (Baker *et al.* 2006). Foxes are adaptable and opportunistic omnivores and are well known for surplus killing and caching of food that is in excess to their requirements (Macdonald & Reynolds 2004; Baker & Harris 2008). Fox diet is eclectic has been relatively well studied by analysis of macro- and microscopic prey remains in scats (Reynolds & Aebischer 1991). Differences in diet have been found between seasons and landscapes (Baker & Harris 2003; Webbon *et al.* 2006), between adults and cubs (Lloyd 1980; Reynolds & Tapper 1995a; Baker *et al.* 2006), and between foxes in neighbouring territories (Reynolds & Tapper 1995a). During the nesting period adult foxes are central place foraging, causing cub diet to be composed of larger prey items as these are preferentially carried back to the earths (Lindström 1994;

Reynolds & Tapper 1995a). This leads to a greater reliance on birds at this time of year, in particular wild Galliformes (i.e. pheasants and partridges, Baker *et al.* 2006). Spring-only fox control appears to be the most effective strategy to reduce this predation pressure.

The least effective strategy with respect to the aim of low nesting period food requirements was autumn-only fox control. Food requirements under this strategy were typically 3-4 times more than under a spring-only strategy due to the timing of culling effort relative to the nesting period, which overlapped only with the last two months. It is important to note that an autumn-only control strategy is more typical where the aim is to improve the survival of reared gamebirds upon release. Many gamekeepers adopt strategies similar to this as they devote their time during spring and summer to hand-rearing of gamebirds (Reynolds & Tapper 1996). Fox predation on recently released pheasants can be substantial (Robertson 1991; Reynolds & Tapper 1995a; Baker *et al.* 2006), and so control efforts to reduce this during the autumn is necessary on released bird estates. As such, improving the productivity of wild stocks is not necessarily the main aim on these estates, so it is perhaps an unfair comparison.

The results indicate that if culling effort is reduced during the nesting period because gamekeeper effort is directed towards rearing, the within-estate food requirements of the fox population will be higher. It is reasonable to expect that wild bird productivity will be worse as a result. It has been shown that in areas where releases of reared pheasants have occurred, wild populations of pheasants are smaller and less productive (Robertson & Dowell 1990; Robertson & Hill 1992). The releasing of birds may have negative effects on wild populations for a number of reasons (Sokos, Birtsas & Tsachalidis 2008), including neglect of other management practices such as predator control (Robertson & Dowell 1990; Arroyo & Beja 2002). Gamebird releasing may have knock-on effects for wild species that are vulnerable to fox predation, such as grey partridge and lapwing, as their productivity will also be expected to suffer from minimal fox control during the nesting period. Gamebird releasing occurs only during a 2-3 month period in late-summer and autumn, but on many estates the numbers released are large enough to ensure shooting is possible until the end of January. This results in an artificially large prey resource for at least six months which

possibly supports more foxes (Chapter 7). The predation pressure on other species during the nesting period may therefore be increased.

This potentially becomes a vicious cycle. In order to supplement a wild stock an estate releases a small number of birds that are mostly lost to predation. More control effort is therefore put into improving survival of these released birds in autumn. This results in the productivity of wild birds being reduced, so more birds to be released to support shooting interests; and so on. Results from the alternative operating model where carrying capacity on an estate was higher or lower relative to the estimated value from the posterior appear to support this view. If K on an estate was higher, e.g. through increased food availability by releasing of birds, then the difference in food requirements between the autumn-only control and the other strategies was also increased as in the absence of control the fox density was able to increase faster and to higher levels during the nesting period. The reverse was true under lower K , when the difference between autumn-only control and other strategies was reduced. Food requirements of foxes under spring-only and year-round strategies were relatively unaffected by differences in K , as there was sufficient culling effort during the nesting period to control the population.

The assumption that immigration was a year-round or seasonal process did not affect the optimal strategy choice. However, under seasonal immigration, nesting period food requirements were lower as no immigration occurred during the April to July period to replace culled foxes. This meant that the difference in food requirements between strategies was reduced, making the most effective strategy less obvious. Simulation modelling of fox populations on restricted areas have previously concluded that immigration is an important factor in the dynamics of culled populations (Harding, Doak & Albertson 2001; McLeod & Saunders 2014). These MSE results show that when immigration rate was reduced to zero on each estate, the food requirements were zero under low effort levels for all strategies. This is because once the resident breeding population was removed following the initial control effort there could be no within-estate cub recruitment and no replacement of foxes by immigration. Lack of control on immigration from neighbouring areas has been cited as the most likely explanation for the failure of fox control on restricted areas (Baker & Harris

2006). These results suggest that collaborative control on neighbouring estates to reduce the source populations of foxes across larger areas may be very beneficial; indeed, it has been shown that fox density can be suppressed at regional scales where culling pressure is high over large areas (Reynolds, Goddard & Brockless 1993; Heydon, Reynolds & Short 2000).

Irrespective of food requirement, the choice of culling strategy has an impact on future population modelling for individual estates. A strategy that is unlikely to produce informative data will not lead to further improvements through adaptive management. Strategies with no lamping effort during the fox breeding season will not provide suitable sighting data to which the model developed in this thesis can be fitted. This would appear to add further support to spring-only and year-round strategies. But the use of low levels of lamping effort at any time of year may also mean that no sightings will be recorded despite the presence of foxes, limiting the ability of the model to estimate the parameters and reconstruct fox density. As the spring-only strategy has six-month periods without any lamping effort, year-round strategies are most likely to provide useful sighting rate data.

8.4.2 Differences between culling methods

Although the spring-only control strategy was consistently the most effective across estates, whether lamping or snaring was the more effective culling method varied between estates. Contrary to expectations, removal of cubs at earths was consistently the least effective culling method across all estates. This was because no adult foxes were removed using this method. Despite a removal of 80% of cubs, if no foxes were removed by other methods the food requirements of the fox population were large due to immigration of adult foxes occurring over the rest of the nesting period. This finding was not influenced by the assumption regarding constant or seasonal immigration although how poor the performance of the method was. Compared to the nesting period food requirement when there was no fox control on DLQ, removal of 80% of cubs (and no lamping or snaring effort) only resulted in a 15% decrease in food required under the constant immigration assumption. Effectiveness improved slightly under the seasonal assumption, with 80% cub removal achieving a 22% decrease in food requirements.

Lamping and snaring were similarly effective on DLQ, with the decrease in nesting period food requirement achieved by each method differing by <2% under all strategies. Observed lamping effort on this estate was low when compared to the range of lamping effort levels considered (8% of maximum annual number of lamping hours). This indicated that proportionally more snaring effort relative to the potential maximum capacity must have been used to achieve the observed degree of control (41% of the maximum annual number of snare nights), suggesting that snaring was viewed as the most important element of the culling strategy implemented by the gamekeeper on this estate. In contrast, the observed level of lamping on VAR was the maximum level of lamping effort considered. For this estate, the model suggests that a more effective use of effort would be to use less lamping effort and run snares at a minimum of 25% of maximum snare density as snares were the more effective method. The results on VAR (and the majority of other estates) also highlight the significant role that snares can have in achieving effective fox control. As already mentioned (8.2.3) snares are a controversial tool. If there were legislative changes to prohibit the use of snares, the ability to undertake effective control on these estates would be compromised, with knock-on effects for prey populations.

The size of VAR meant that at the maximum snare density, the number of snare nights on VAR (48,412 snare nights per year) was many times greater than the number of snare nights in use on DLQ (6,552 snare nights per year). This raises the question of whether large numbers of snares can be checked daily by a single gamekeeper to both remain within the law (it is a legal requirement to check snares at least once daily) and comply with the snaring Code of Practice (Defra 2005). The greatest number of snares known to be checked daily by a gamekeeper in the GWCT trial was 391, with a mean of 268 snares. It must therefore be presumed that it is possible to run this number of snares though it is not known whether the gamekeeper on this estate followed the Code of Practice, which recommends two checks per day and to set snares only when there is evidence of fox presence and the risk of non-target capture is low. The maximum snaring effort on VAR would imply 133 snares per night for year-round strategies and 267 or 265 snares per night for spring- and autumn-only control, respectively. These numbers of snares are thus on the limit of what is known to be possible to consistently check daily. For the largest estate

(GDE), the maximum snaring effort considered would equate to 72,436 snare nights per year: under a spring- or autumn-only strategy the number of snares required (400 or 396 snares per night, respectively) would appear to be more than can be managed by a single gamekeeper consistent with good practice. However, on these estates (GDE, VAR) snaring was by far the most effective method and similar effects on nesting period food requirements were achieved at levels of snaring 25-50% of the maximum. Running snares at the maximum density considered is therefore not necessary.

The relative effectiveness of lamping and snaring (DLQ = both, OCS = lamping, VAR = snaring) can be explained given the parameter values on each of these estates. The rate of successful search was similarly low on DLQ, OCS and VAR, suggesting that this parameter was not important in determining the effectiveness of lamping effort as these estates differed greatly with respect to this. Of more importance were the parameters key to determining density, such as immigration rate and carrying capacity. DLQ was included in the reference set of estates because of a high estimate of ν . Snaring and lamping were similarly effective on DLQ, as was the situation on the other estate where ν was high, YEM. In contrast, ν was low on VAR and snaring was the more effective method. This leads to the conclusion that lamping is more effective on estates where ν is higher. However, it is not quite this simple, as ν was also low on OCS where lamping was the most effective method. OCS was included in the reference set of estates because of a high estimate of carrying capacity. K was also fairly high on DLQ and YEM, where lamping was similarly effective to snaring. The estimate of per capita birth rate was also higher on OCS than on VAR so cub recruitment would be higher if foxes were present to breed, thereby reducing the effect of low ν and improving the effectiveness of lamping. Populations with high values of K , ν and r will all tend to have higher fox density, which appears to improve the effectiveness of lamping relative to snaring. The reasons for this are unknown.

The relative effectiveness of culling methods on different estates reflects the assumptions made by the model. The values of the rate of successful search are estate-specific but the large difference in lamping effectiveness between estates with similar values for d suggests that the effect of scale of this parameter is only minimal. If there was

evidence of seasonality in the rate of successful search that could be incorporated into the model, rather than assuming that d is constant over time; this might then alter the ranking of both strategies and culling methods on an estate. The most likely situation is that d is lower during the nesting period because crop growth reduces the detection probability; if so, it would be expected that as a result of seasonally variable d the performance of year-round strategies would improve the most. Further empirical work is required to determine whether there is seasonal variation in d . The probability of a sighted fox being killed and the probability of snaring success per fox were assumed to be the same across estates and so were not expected to influence the effectiveness of either method on each estate. Tailoring these parameters to the skills of the gamekeepers working on the estates would improve the realism of the results, but this would require large amounts of extra data. p_k and p_s were also assumed to be constant over time. If for any reason these values were lower during the fox breeding period then the relative effectiveness of removal of cubs at earths would be increased, and *vice versa*.

It has been shown elsewhere that the cost of catching each fox increases as fox density decreases (Kay *et al.* 2000). Quantifying the most efficient method would allow better decisions to be made about which method to use; for example, if lamping and snaring are similarly effective on an estate but snaring is significantly less expensive, then – on an economic argument alone – resources would be better directed towards snaring effort. Such an assessment of the cost-efficiency of each effort level scenario was not possible here as each culling method was in different units of effort. There is little point in making assumptions about how many snares can be checked in a given time, but maintenance of snares and handling of captured animals will depend on density of both foxes and non-target species. Improved understanding of the costs of each culling method across a range of fox populations of different densities and ecological conditions would be useful to enable a more detailed cost/benefit analysis to be undertaken.

8.4.3 Trade-offs

Management decisions about a fox population control strategy, as with control of any predator or pest species, inevitably come down to trade-offs based upon three considerations: 1) effectiveness, or how well the control strategy achieves its aims, e.g. reduced food requirements; 2) efficiency, in terms of economic cost, specificity to target species, and economy in numbers of animals killed; and 3) humaneness (Reynolds & Tapper 1996; Baker & Harris 2006). These trade-offs are delicately balanced, with effectiveness ultimately constrained by requirements for efficiency and humaneness. The trade-offs identified in this chapter related to feedback, number of foxes killed, and timing of control reflect this balance and are discussed below.

The use of feedback on the status of the population size to guide culling effort does not appear to be as effective at reducing fox population food requirements as the naïve use of culling effort, i.e. without feedback. This is because under the naïve approach the amount of culling effort used each week is at the maximum of what is available within a given scenario of effort levels. This is the same amount of effort that is used if the feedback approach determines that culling should take place in a given week. Because there are weeks without culling effort under the feedback approach, immigration means that the fox population can begin to recover and so the food requirement is higher. If a more complicated culling control model was used that adjusted the culling effort used in some way in response to feedback, e.g. the effort response was based upon the number of scats found during the search, only then could the feedback approach improve upon the naïve approach of achieving the aim of reduced fox food requirements.

Given enough hours of scat search effort per week, the difference between the levels of control achieved with and without feedback was relatively small under all control strategies. However, the amount of culling effort used may be considerably less with feedback. Spring-only control was shown to be the most effective strategy at reducing nesting period food requirements. Spring- and autumn-only control are the strategies that result in the greatest effort savings through use of feedback; year-round control strategies

result in smaller effort savings because there are potentially more weeks during the year in which effort may be used. Maintaining effectiveness and improving efficiency of culling through strategy choice is clearly desirable. For methods such as snaring, use of less effort by setting snares in response to fox presence is advised in the Code of Practice (Defra 2005), and by using fewer snares the risk of non-target capture (or injury) is much reduced. The effort savings from use of feedback are expected to become greater as fox density decreases because there will be fewer foxes to remove. Savings in culling effort must be balanced with costs of search effort, but search effort may not present an additional cost if it is undertaken by gamekeepers whilst walking around the estate to perform other tasks.

Targeted fox control during the spring may thus represent a good trade-off between effectiveness and all aspects of efficiency, at least for estates that do not have such high harvest targets as to require the use of reared gamebirds to reach the target. But the decision depends on the species that control is aiming to benefit. When compared to naïve use of effort without feedback on DLQ, the increase in food required during the nesting period when eight hours per week were spent searching for scat was about 15 kg across the entire 3.2 km² estate. This is equivalent to about 12 pheasants, but 44 grey partridges. As a nationally threatened species (Eaton *et al.* 2009), the implications for grey partridges would be the more damaging in conservation terms. In such situations the naïve use of control to maintain effectiveness may be preferred despite the costs to efficiency and humaneness.

There were also trade-offs related to the numbers of foxes killed under different strategies. Not only was spring-only control the most effective strategy at reducing nesting period food requirements, it was also the most efficient in terms of the number of foxes that were culled annually to achieve this degree of control. Fox culls were lower under spring-only compared to year-round control because 1) the relative intensity of culling effort meant that the adult fox population was greatly reduced just prior to the fox breeding season, so that cub recruitment was minimal; and 2) there was not the cost of continual removal of immigrant foxes during the autumn and winter (Reynolds, Goddard & Brockless 1993). Choice of method is also affected by this trade-off. From the example using a spring-only strategy on DLQ, when used on its own lamping was only slightly more effective at reducing

the nesting period food requirement than snaring. However, lamping was considerably less efficient as 24% more foxes had to be culled annually.

The different control strategies dictate that culling will occur at different times throughout the year. Spring-only and year-round control strategies both involve culling of adults during the fox breeding season, which carries the extra welfare cost of orphaning dependent cubs (Reynolds 2004). This is therefore a direct trade-off between the ability to do effective control to benefit wild prey, and humaneness. There is also a trade-off between achieving effective nesting period control and over-winter food requirements of the fox population. The spring-only strategy allows the fox population to recover to relatively high densities over-winter via immigration. This may have adverse consequences on vulnerable prey species via winter predation; in situations where this is important a year-round control strategy might be more appropriate to protect prey populations. Conversely, foxes may be beneficial to the agricultural interests on shooting estates where prey species are pests (Baker & Harris 2003; Macdonald *et al.* 2003). Agricultural pest species vulnerable to fox predation include rats and rabbits; it has been shown that rabbit abundance is inversely related to fox control (Trout *et al.* 2000). This implies that periods without fox control, e.g. use of a spring-only strategy, could bring unexpected benefits.

8.4.4 Extensions

By capturing the key dynamics of a population, its observation and monitoring, and the setting and implementation of control rules, MSE enables a comparison of the performance of alternative management strategies when making decisions under uncertainty. The approach was developed by the International Whaling Commission during the late 1980's to reduce the risk of commercial overharvesting of baleen whales (Kirkwood 1997). It has been widely applied in fisheries management since then (Butterworth & Punt 1999; Smith, Sainsbury & Stevens 1999; Sainsbury, Punt & Smith 2000; Kell *et al.* 2006). Recently, terrestrial applications of MSE are becoming more prevalent for conservation, e.g. subsistence harvesting of bushmeat (Milner-Gulland 2011) and setting of trophy hunting quotas for African lion (Edwards *et al.* 2014). MSE has also been applied in a pest control

context, e.g. in the control of overabundant kangaroo populations (Chee & Wintle 2010). In many of these applications of MSE, the harvest control rules are based upon the results of an annual assessment of resource status. As such, model-based MSE is most commonly applied as this incorporates the assessment process (McAllister *et al.* 1999). In contrast to these applications, culling control rules in this chapter's application to fox populations are on within-year time-steps. This would require a much greater number of assessment models to be fitted. In addition, an assessment of a fox population is not economically viable on annual time-steps, let alone multiple times a year. While it was an option, model-based MSE was not applied to fox populations for these reasons. The model-free approach has the added advantages of being (slightly) simpler to explain to decision makers and stakeholders, i.e. gamekeepers and estate owners, and requiring less computation time (McAllister *et al.* 1999; Rademeyer, Plagányi & Butterworth 2007), although computation time for harvest control rule problems in fisheries can be greatly reduced by using Kalman filter approximations for the dynamic state estimation process in model-based approaches (Walters 2004).

Implementation uncertainty was not considered in the MSE applied to foxes as it was assumed that gamekeepers would use the maximum effort available under each scenario to cull as many foxes as possible. Nonetheless there may be instances where this assumption fails, e.g., if the lamping vehicle or spotlight broke to prevent lamping effort being used. Contrarily, some gamekeepers might choose to use more effort as they perceive the risk from fox predation to be higher and this may affect the balance between trade-offs. Recent work has sought to quantify implementation uncertainty with regards to recreational hunters failing to fulfil annual harvest quotas for large carnivores (Bischof *et al.* 2012). An extension to this application of MSE to fox population control could therefore incorporate implementation uncertainty. Improvements to terrestrial conservation and management applications of MSE may also come from incorporation of human decision making into implementation models using household utility functions (Milner-Gulland 2011). This approach might be useful in modelling and evaluating the outcomes of the behaviour of different gamekeepers and their individual decisions about fox control.

8.5 Tables

Table 8.1. Symbols and description for model parameters and variables used in this chapter.

Notation	Description
<i>Subscripts</i>	
t	Time, weekly time-step
a	Adult component of lampable population
j	Juvenile component of lampable population
m	Male component of lampable population
f	Female component of lampable population
<i>Known parameters</i>	
A	Estate area, km ²
$b_{a,t}, b_{j,t}$	Indicator of adult or juvenile immigration
w_t	Proportion of cubs on an estate weaned
φ	Male-to-female sex ratio
<i>State parameters</i>	
N_0	Fox density in week 0, fox km ⁻²
K	Fox density at carrying capacity, fox km ⁻²
ν	Immigration rate, fox km ⁻² wk ⁻¹
r	Per capita birth rate, cub fox ⁻¹ yr ⁻¹
M	Instantaneous non-culling mortality rate, wk ⁻¹
<i>Observation parameters</i>	
d	Rate of successful search, km ² hr ⁻¹
p_k	Probability of a sighted fox being killed
p_s	Probability of snaring success per fox per week
p_c	Probability of being killed at the earth per cub
f	Probability of fox capture per snare per day
<i>Error terms</i>	
σ_p	Standard deviation in process error (time-step specific)

Continued on next page

Table 8.1 continued

Notation	Description
<i>States</i>	
$N_b, N_{a,b}, N_{j,b}, N_{m,b}, N_{f,t}$	Fox density, fox km ⁻²
ε_t	Weekly process error
h_t	Bernoulli random variable determining order of culling
<i>Culling data</i>	
E_t	Hours of lamping effort
Y_t	Number of foxes sighted
$L_b, L_{a,b}, L_{j,t}$	Lamping cull, fox km ⁻²
s_t	Number of snare nights
$S_b, S_{a,b}, S_{j,t}$	Snaring cull, fox km ⁻²
C_t	Cub cull at earths, cub km ⁻²
<i>Observation model parameters and indices</i>	
QW	Length of linear features walked per week, km
QA	Length of linear features on estate, km
QL	Length of linear feature per km ² in Environmental Zone, km
T	Number of scat search hours per week
V	Walking speed, kmh
R	Defecation rate, scats fox ⁻¹ wk ⁻¹
PL	Proportion of scat deposited in linear features
PF	Proportion of scat present in linear features detected
FL	Number of scats present in linear features
F_t	Number of scats found per week
U_t	Index of sighted foxes not killed

Table 8.2. Posterior median parameter values for estates to which MSE was applied. Low values relative to other estates are shown in italic and high values are shown in bold.

Estate	Area, km ²	<i>K</i> , fox km ⁻²	<i>v</i> , fox km ⁻² wk ⁻¹	<i>r</i> , cub fox ⁻¹ yr ⁻¹	<i>M</i> , wk ⁻¹	<i>d</i> , km ² hr ⁻¹
DLQ	3.2	6.56	0.18	3.11	0.0086	<i>0.20</i>
GDE	36.4	<i>2.57</i>	0.10	<i>2.75</i>	0.0093	0.77
GHT	5.7	6.19	0.14	2.04	0.0085	<i>0.20</i>
HIR	6.1	2.74	0.14	2.99	0.0096	0.22
HUS	9.3	<i>1.98</i>	0.07	3.63	0.0102	0.36
NYP	10.1	4.55	0.15	<i>2.52</i>	<i>0.0070</i>	0.42
OCS	1.6	8.47	0.06	3.32	0.0085	0.22
VAR	24.3	3.34	<i>0.04</i>	<i>1.16</i>	0.0092	0.21
YEM	4.3	6.30	0.56	<i>1.92</i>	<i>0.0072</i>	0.30

Table 8.3. Environmental Zone and length of linear feature on each estate.

Estate	Environmental Zone	Length of linear feature per 1-km square, km	Area, km²	Total length of linear feature on estate, km
DLQ	1	11.022	3.2	35.3
GDE	6	12.868	36.4	468.4
GHT	1	11.022	5.7	62.8
HIR	1	11.022	6.1	67.2
HUS	1	11.022	9.3	102.5
NYP	2	8.047	10.1	81.3
OCS	1	11.022	1.6	17.6
VAR	1	11.022	24.3	267.8
YEM	2	8.047	4.3	34.6

8.6 Figures

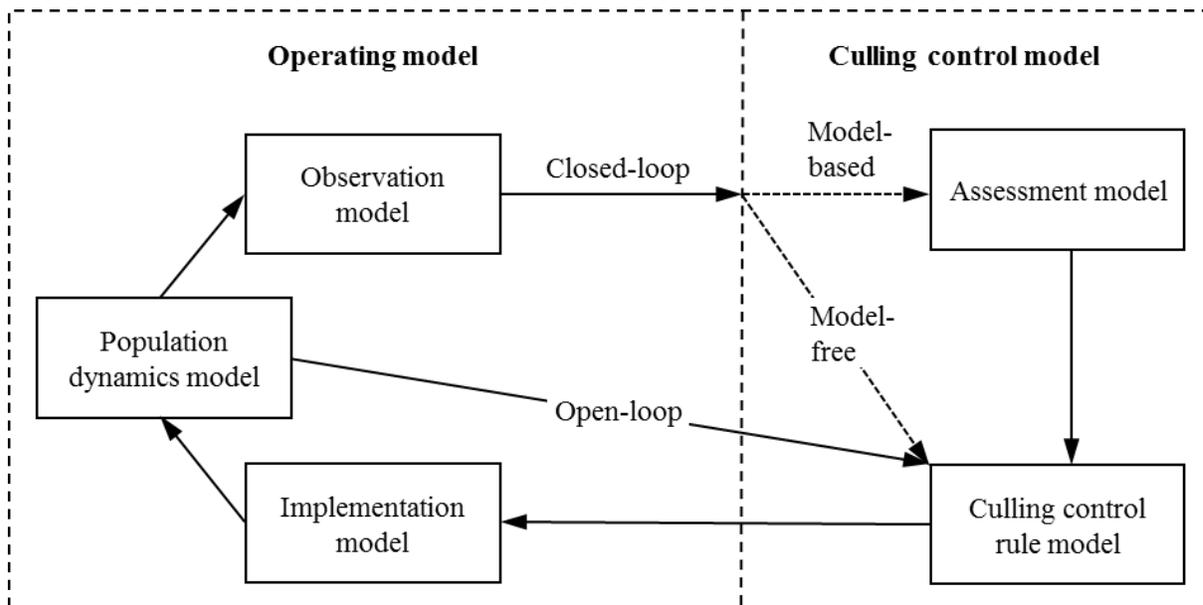


Figure 8.1. The main model components in a management strategy evaluation. Note the different pathways of open- and closed-loop feedback control and model-free and model-based culling control models.

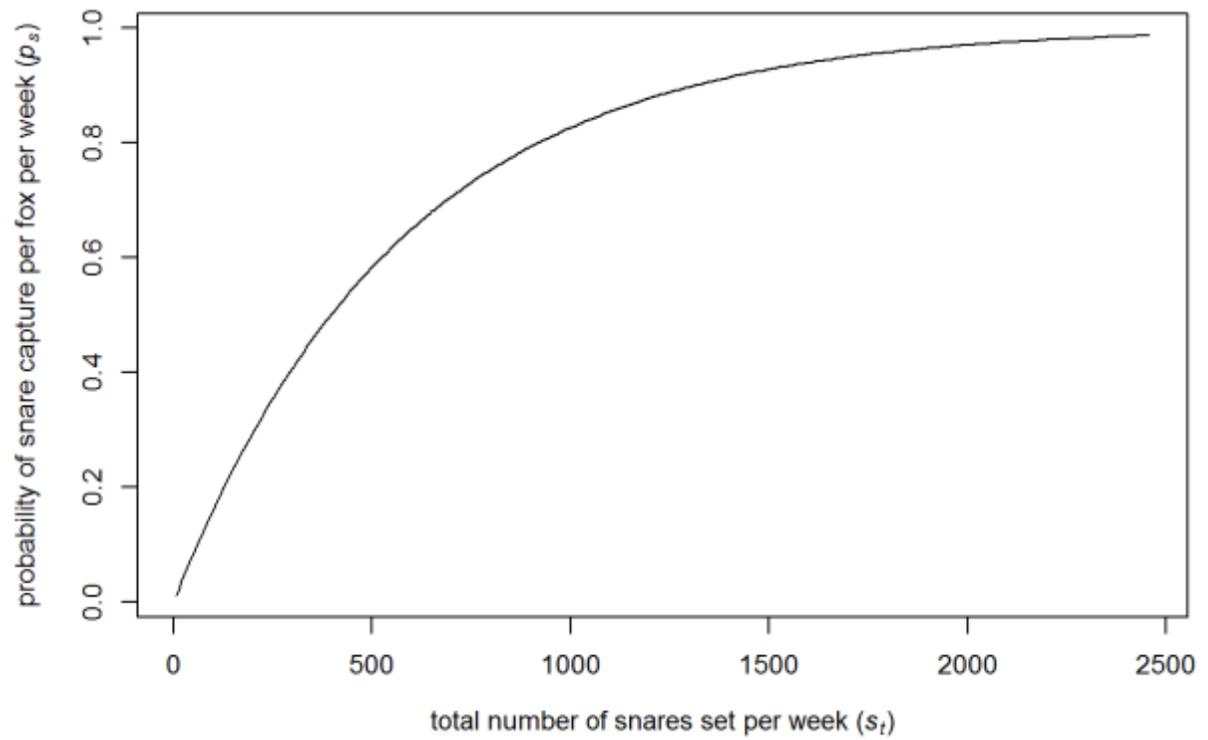


Figure 8.2. Cumulative distribution function of the geometric distribution describing the probability that one fox is captured by snares given a number of snare nights in a week.

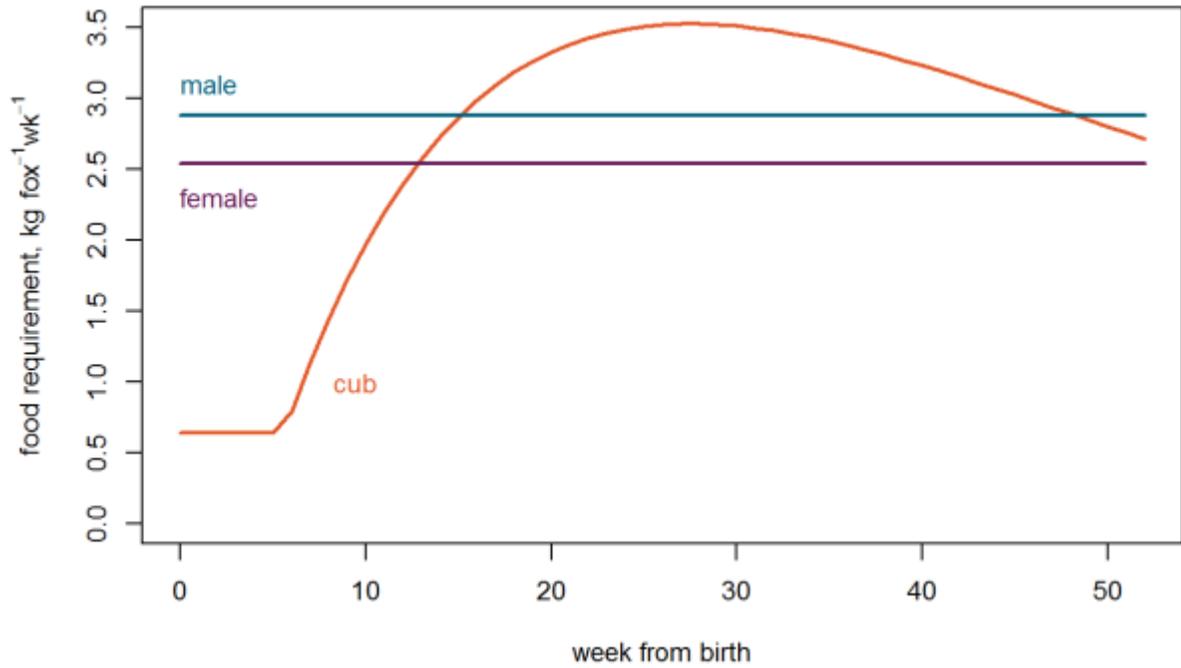


Figure 8.3. Weekly food requirement of individual fox cubs during their first year. Adult male and female fox food requirements are shown as a reference. Curves are based upon data from Sargeant (1978), adjusted for British foxes.

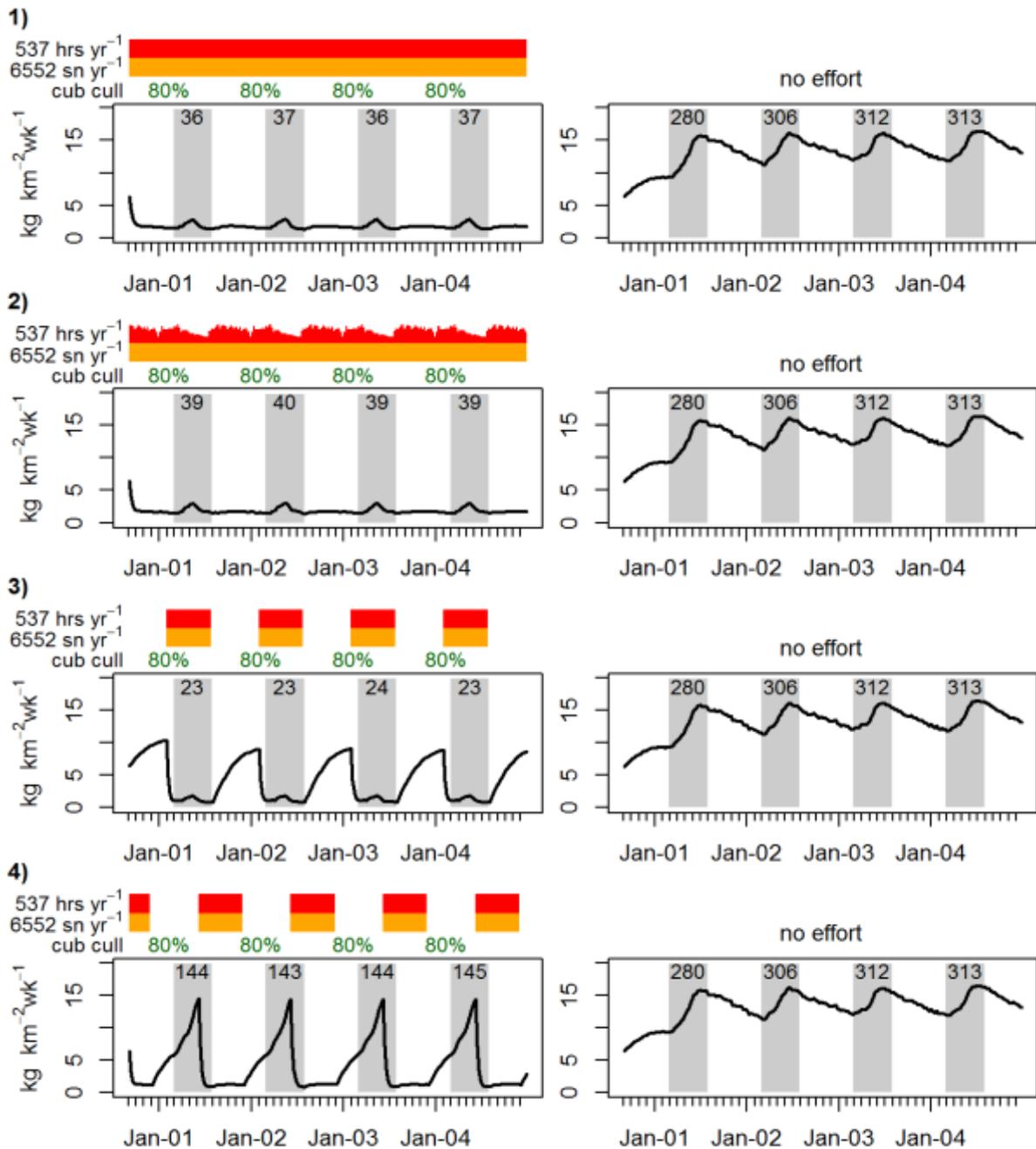


Figure 8.4. Results from open-loop management strategy evaluation showing the food requirement of the fox population on DLQ under maximum levels of culling effort for each strategy: 1) year-round uniform, 2) year-round with seasonal lamping effort, 3) spring (Feb-Jul) control only, and 4) autumn (Jun-Nov) control only. Food requirements under each strategy (left) are compared with the food requirement of foxes given no culling effort (right). Red and orange bands indicate the timing of culling effort and relative level of lamping effort. The nesting period is shown in grey as a reference. Numbers shown within the nesting period indicate the total food requirement (in kg km^{-2}) of the fox population during this period.

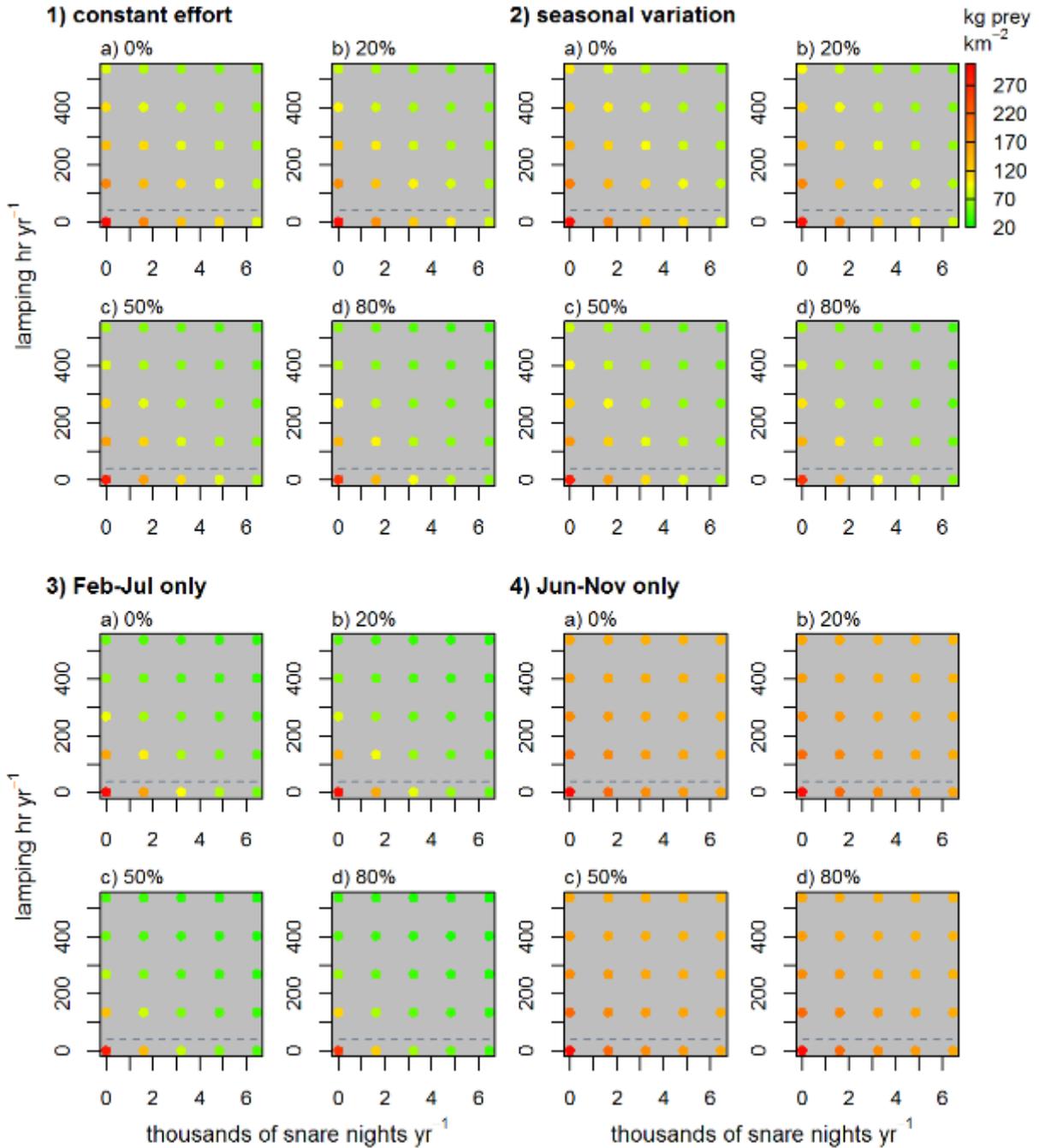


Figure 8.5. Scatterplots showing results of open-loop management strategy evaluation for DLQ under different levels of culling effort. Colour scale ranges from high food requirements (red) to low food requirements (green). Figures are arranged in sets of four by strategy 1) year-round uniform, 2) year-round with seasonal lamping variation, 3) spring (Feb-Jul) control only, and 4) autumn (Jun-Nov) control only. Figures a)-d) within each strategy set refer to different percentages of cubs killed at earths. Dashed horizontal lines show the mean observed level of lamping effort on this estate.

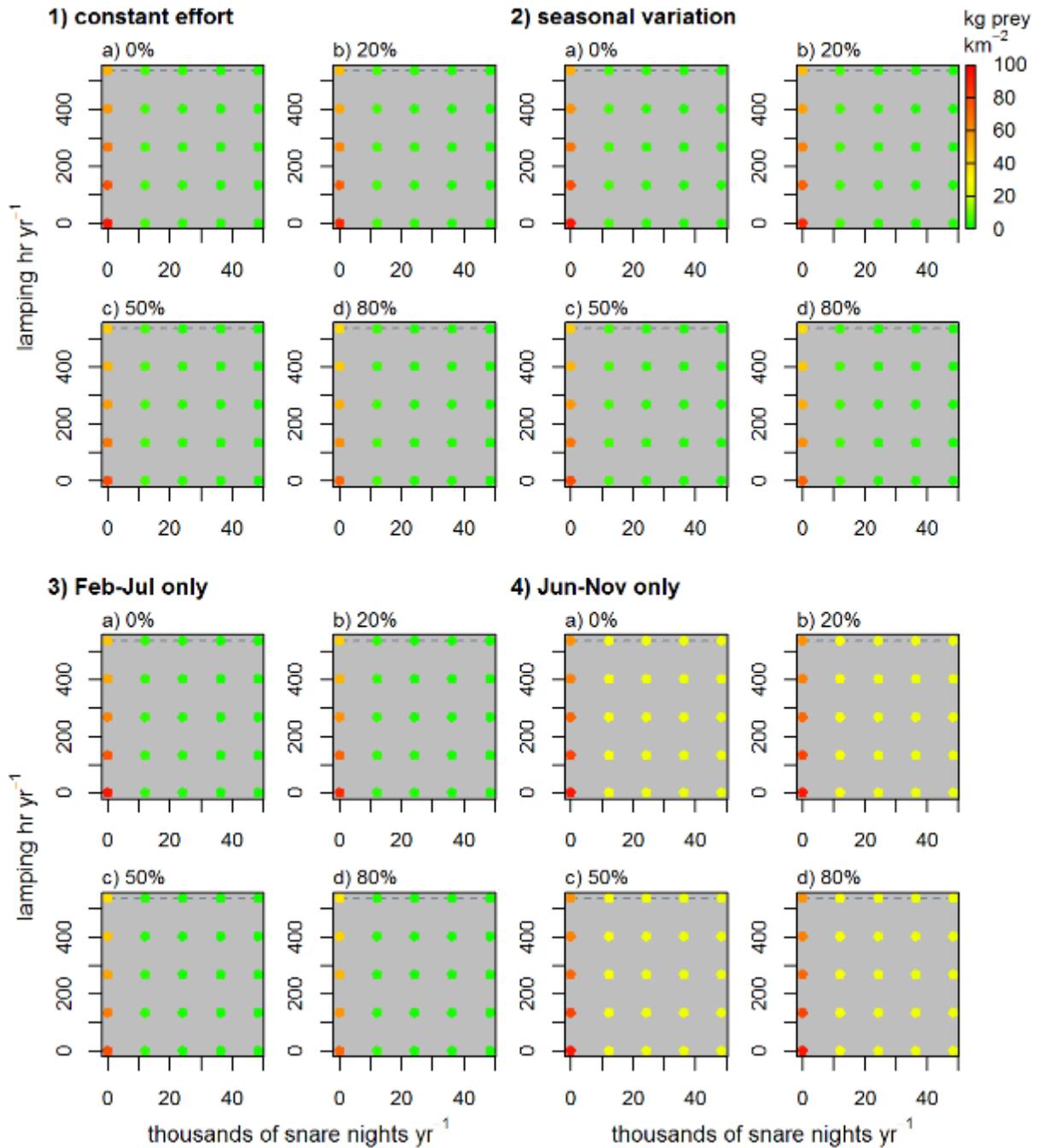


Figure 8.6. Scatterplots showing results of open-loop management strategy evaluation for VAR under different levels of culling effort. Colour scale ranges from high food requirements (red) to low food requirements (green). Figures are arranged in sets of four by strategy 1) year-round uniform, 2) year-round with seasonal lamping variation, 3) spring (Feb-Jul) control only, and 4) autumn (Jun-Nov) control only. Figures a)-d) within each strategy set refer to different percentages of cubs killed at earths. Dashed horizontal lines show the mean observed level of lamping effort on this estate.

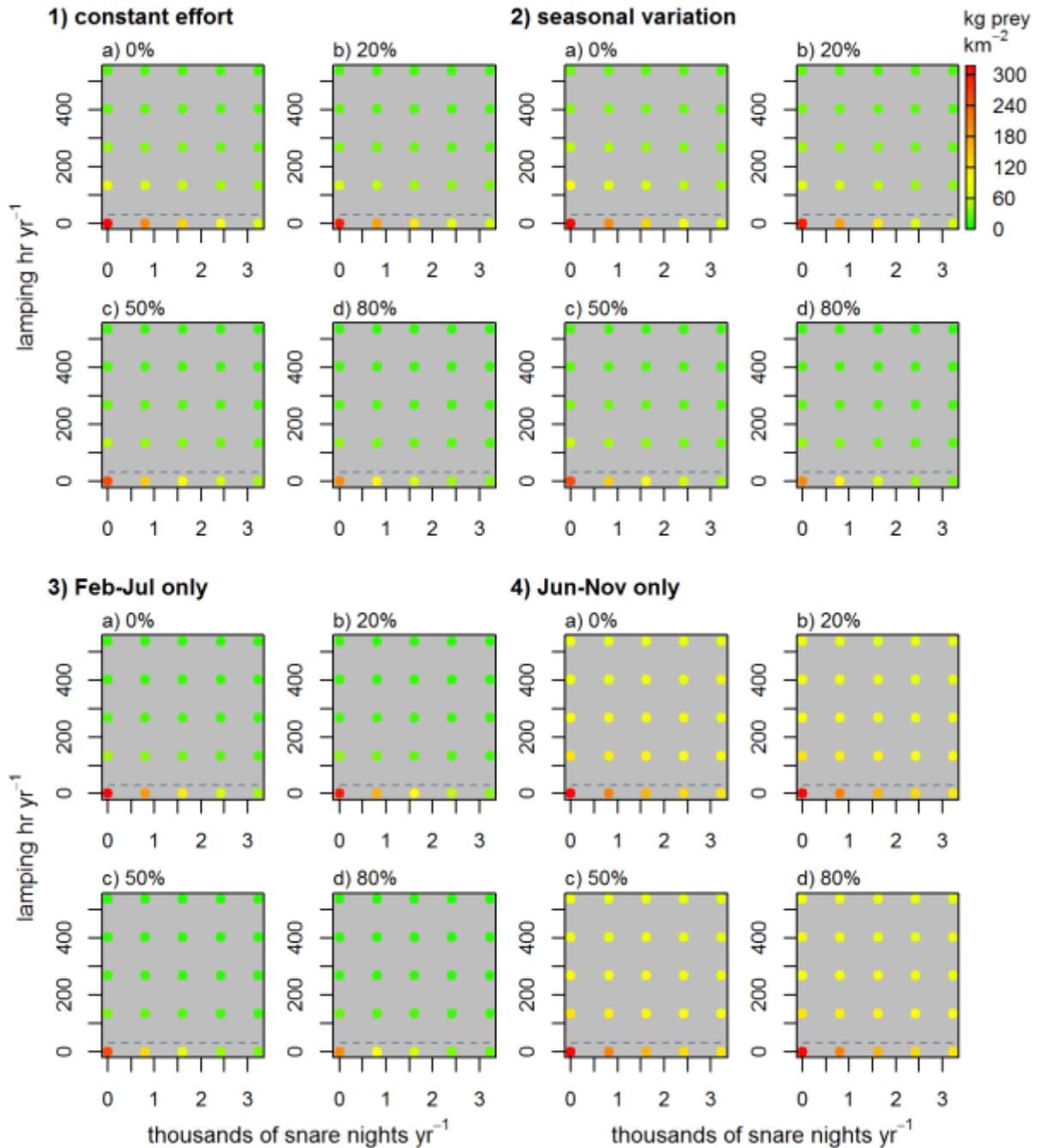


Figure 8.7. Scatterplots showing results of open-loop management strategy evaluation for OCS under different levels of culling effort. Colour scale ranges from high food requirements (red) to low food requirements (green). Figures are arranged in sets of four by strategy 1) year-round uniform, 2) year-round with seasonal lamping variation, 3) spring (Feb-Jul) control only, and 4) autumn (Jun-Nov) control only. Figures a)-d) within each strategy set refer to different percentages of cubs killed at earths. Dashed horizontal lines show the mean observed level of lamping effort on this estate.

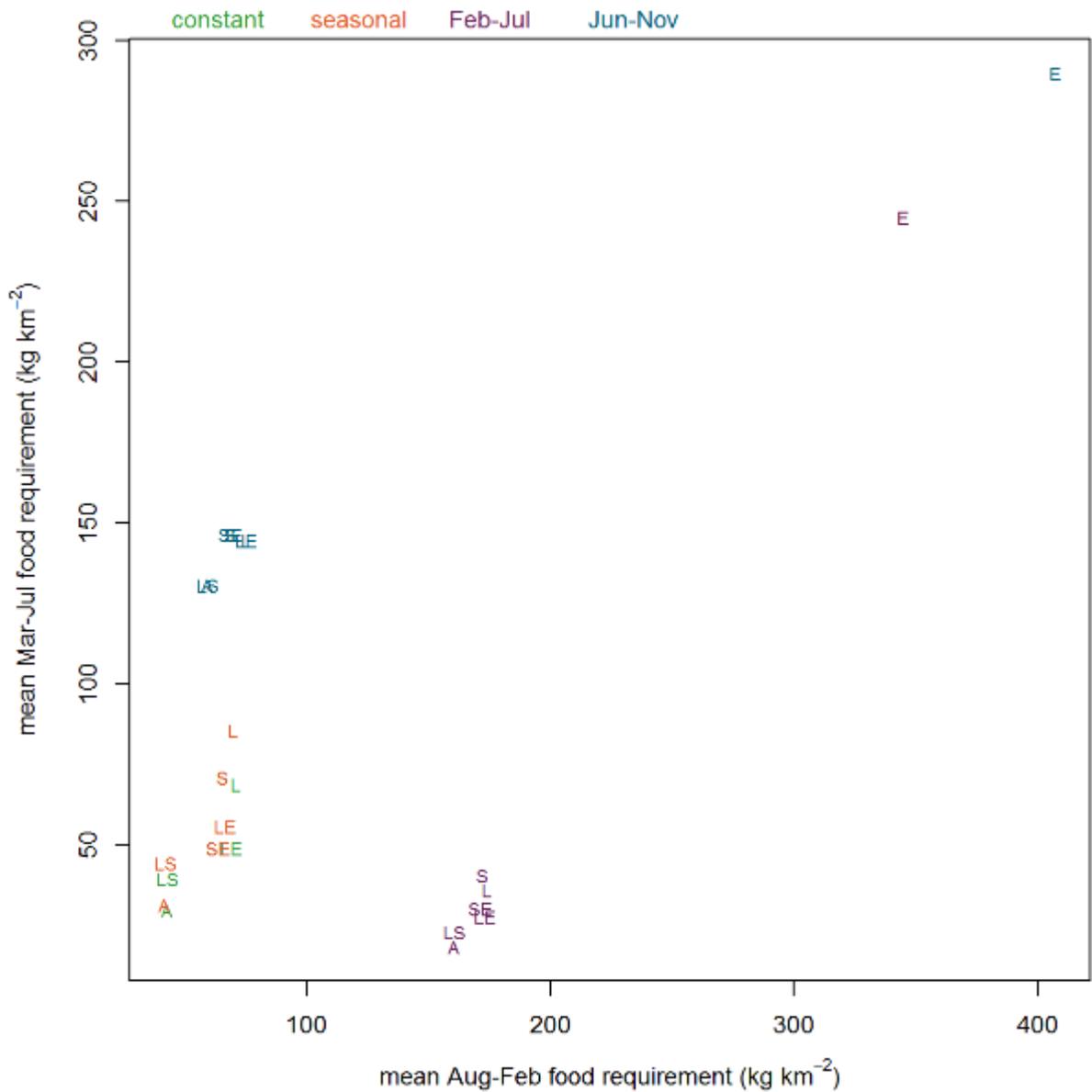


Figure 8.8. Trade-offs between nesting period food requirements and food required during the rest of the year under different combinations of culling methods on the DLQ estate. Letters refer to each culling method (or combination thereof): L = lamping, S = snaring, E = cubs killed at earths, A = all methods. Results are from open-loop MSE and are shown under the maximum levels of effort for each method.

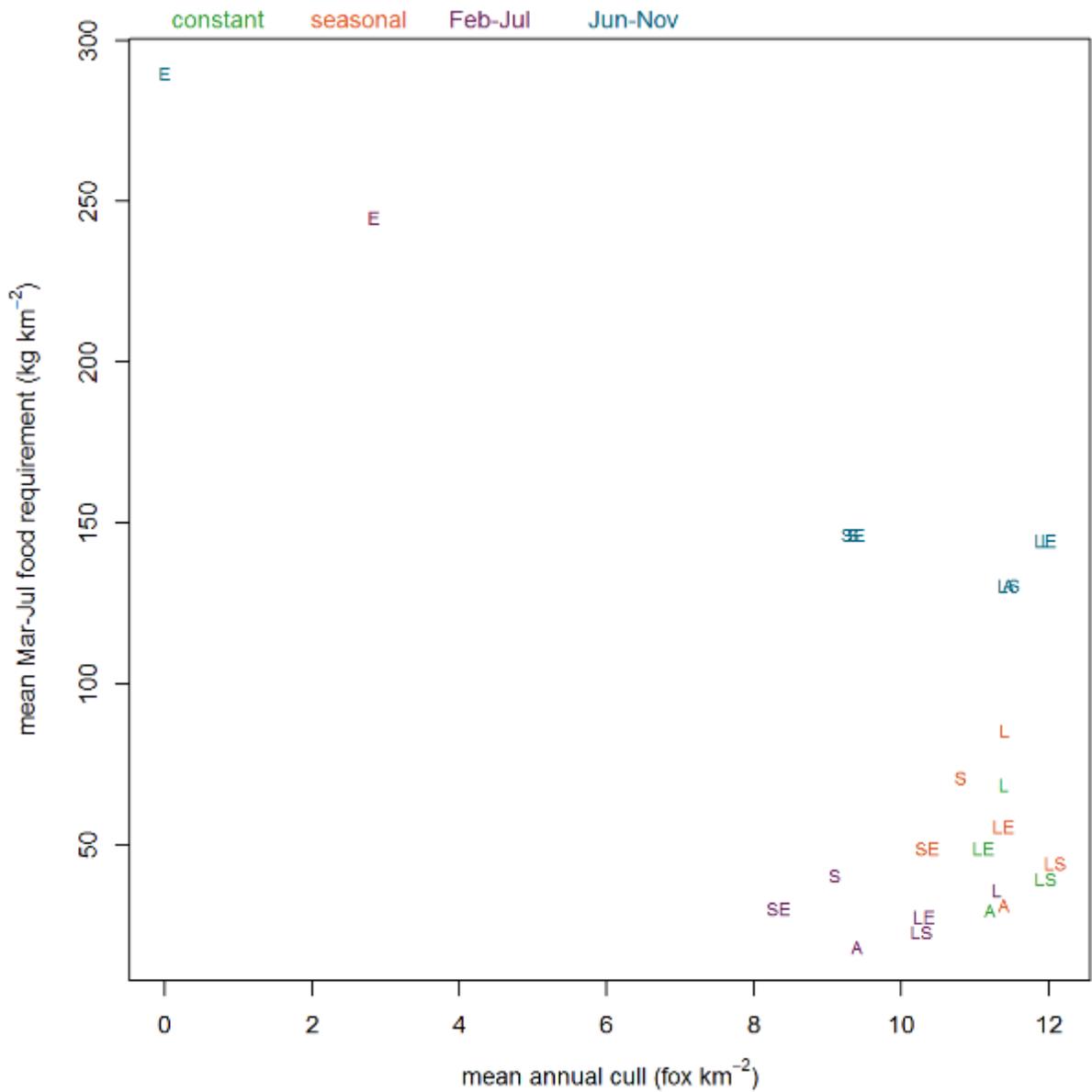


Figure 8.9. Trade-offs between the effectiveness of different combinations of culling methods at reducing the food requirement during the nesting period and the number of foxes which must be killed annually to achieve this level of control on the DLQ estate. Letters refer to each culling method (or combination thereof): L = lamping, S = snaring, E = cubs killed at earths, A = all methods. Results are from open-loop MSE and are shown under the maximum levels of effort for each method.

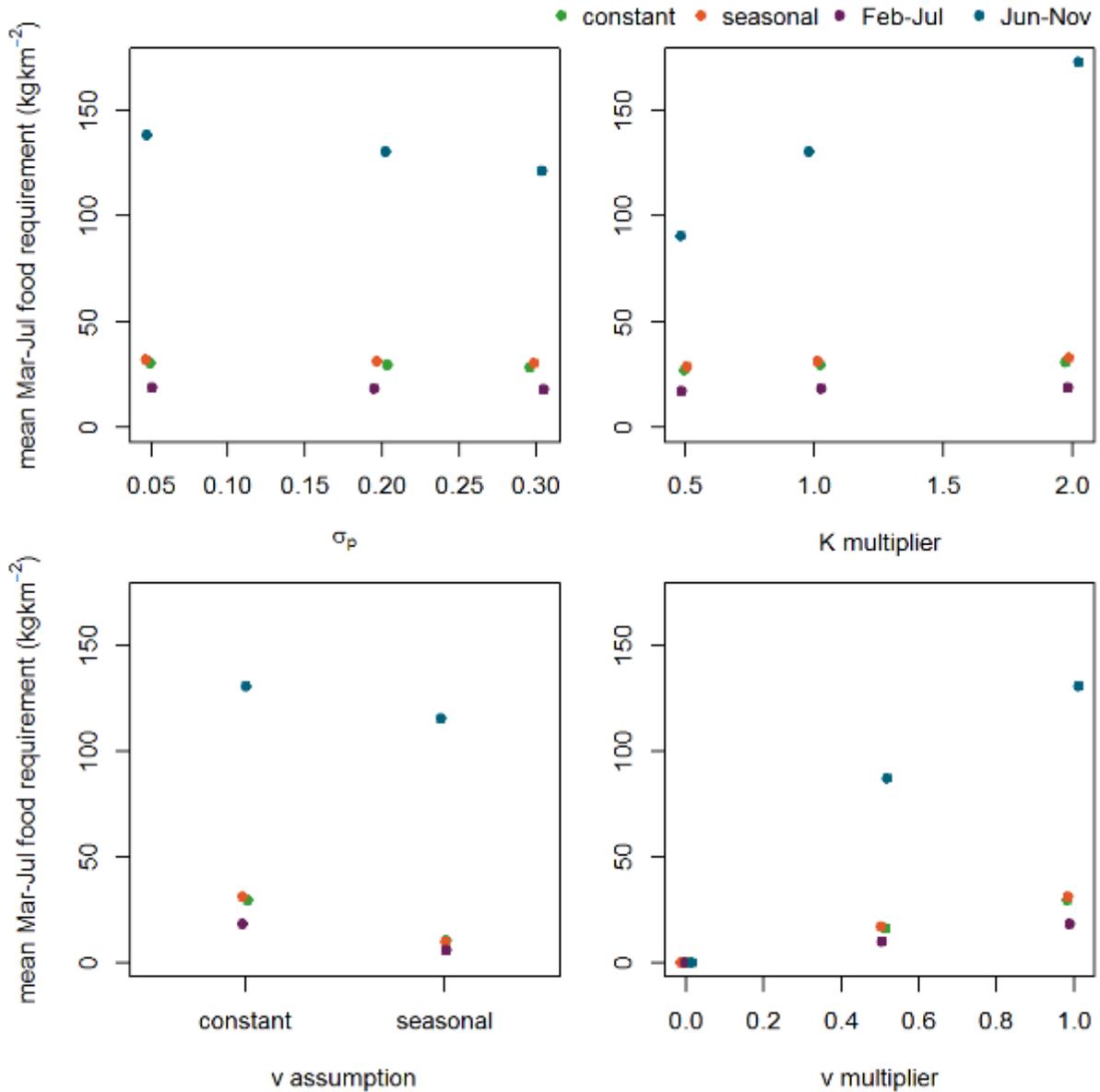


Figure 8.10. Sensitivity of results on the DLQ estate to different assumptions about the standard deviation in process errors (σ_p) on a two-weekly time-step; the effect of assuming that immigration is a constant process throughout the year or is a seasonal process that occurs during the fox dispersal period; the effect of a higher or lower carrying capacity; and the effect of lower or zero immigration. Results are from open-loop MSE and are shown under the maximum levels of effort for all methods. Points are jittered around the x-values in each panel so that underlying points can be seen.

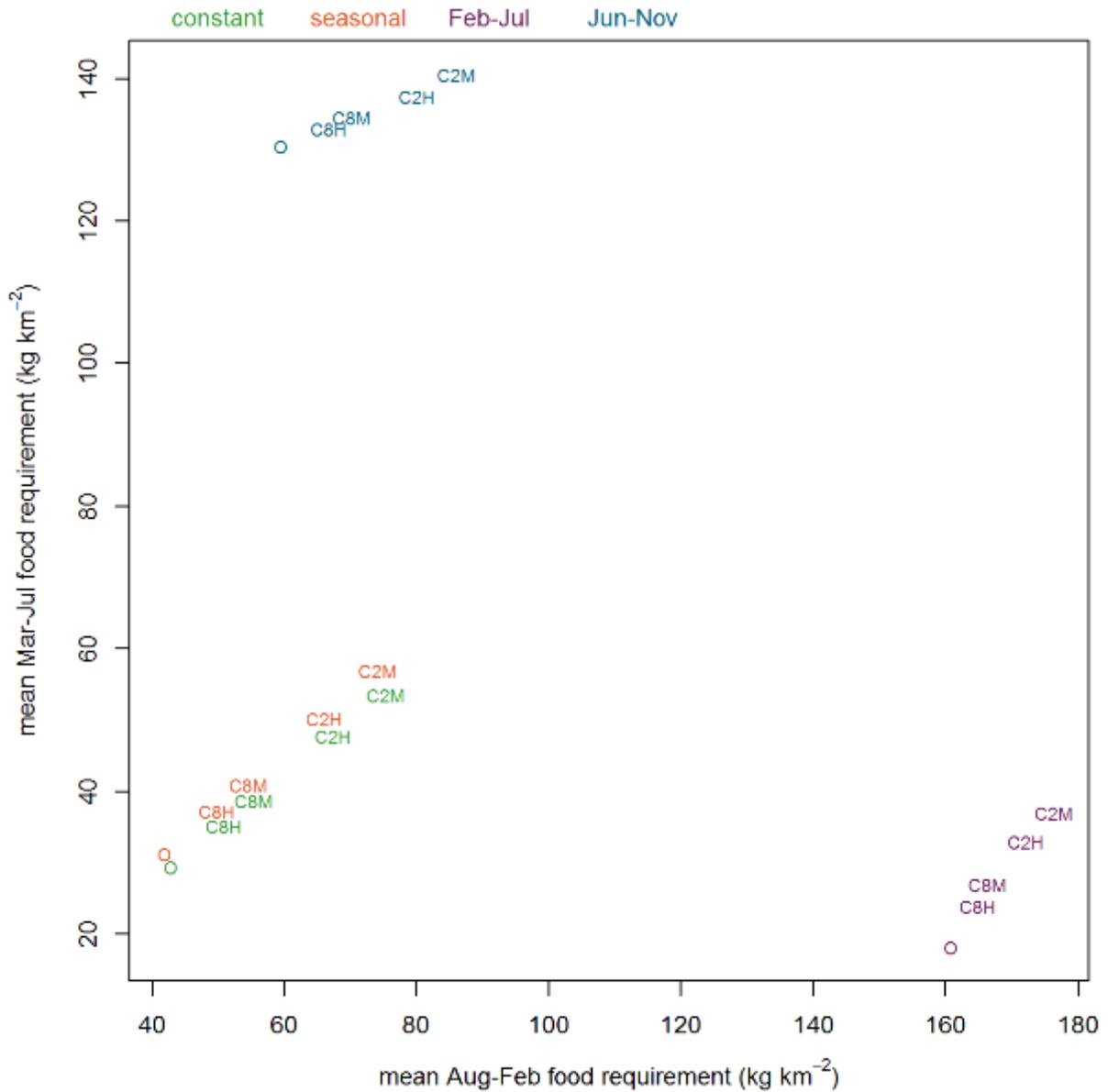


Figure 8.11. Trade-offs between nesting period food requirements and food required during the rest of the year under open-loop (O) and closed-loop (C) MSE on the DLQ estate. For closed-loop options, numbers 2 or 8 refer to the number of search hours per week, letters M or H refer to the probability of finding scats if present (Medium = 0.5, High = 0.8). Results are shown under the maximum levels of effort for all methods.

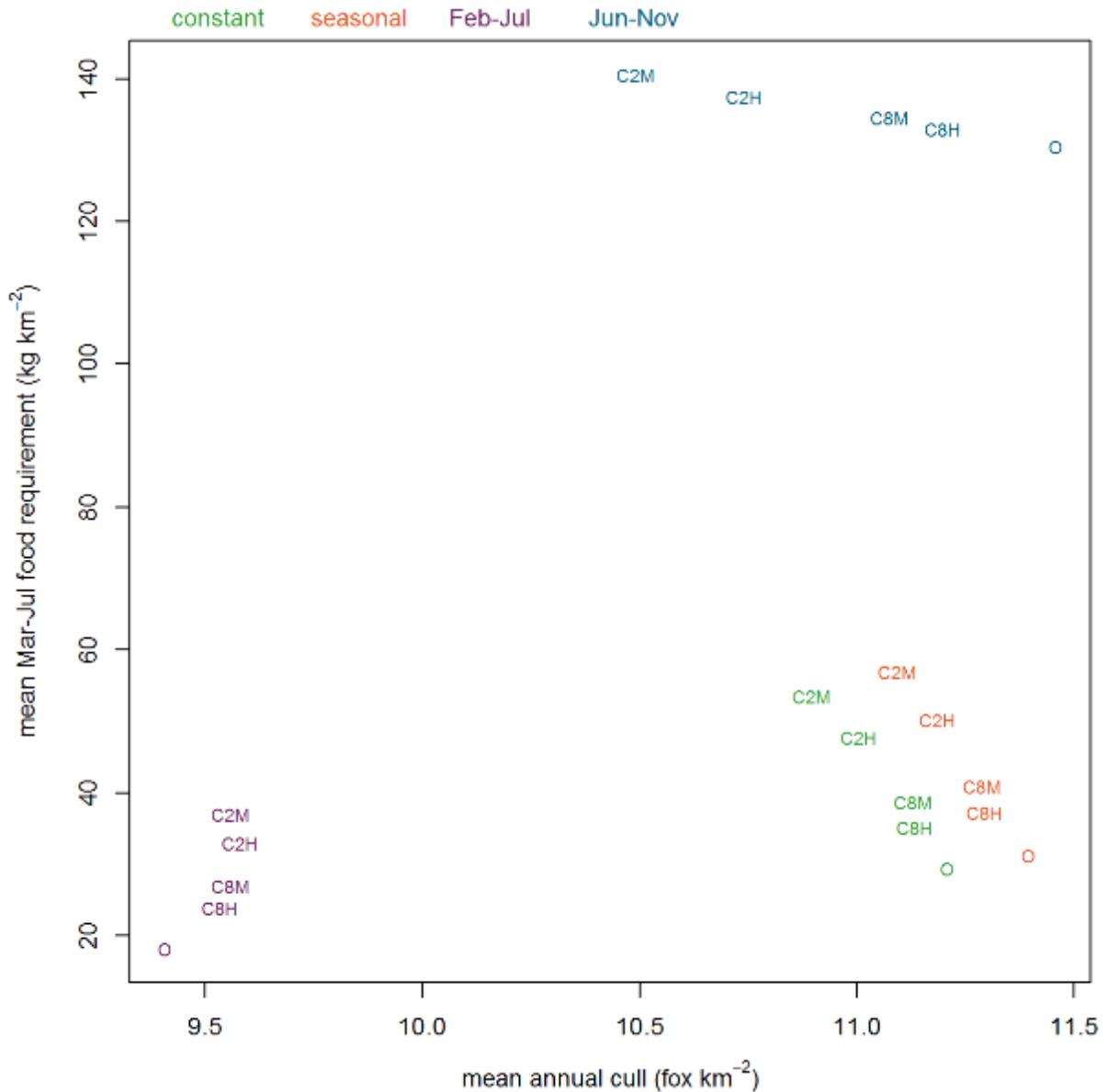


Figure 8.12. Trade-offs between the food requirement during the nesting period and the number of foxes which must be killed annually to achieve this level of control under open-loop (O) and closed-loop (C) MSE on the DLQ estate. For closed-loop options, numbers 2 or 8 refer to the number of search hours per week, letters M or H refer to the probability of finding scats if present (Medium = 0.5, High = 0.8). Results are shown under the maximum levels of effort for all methods.

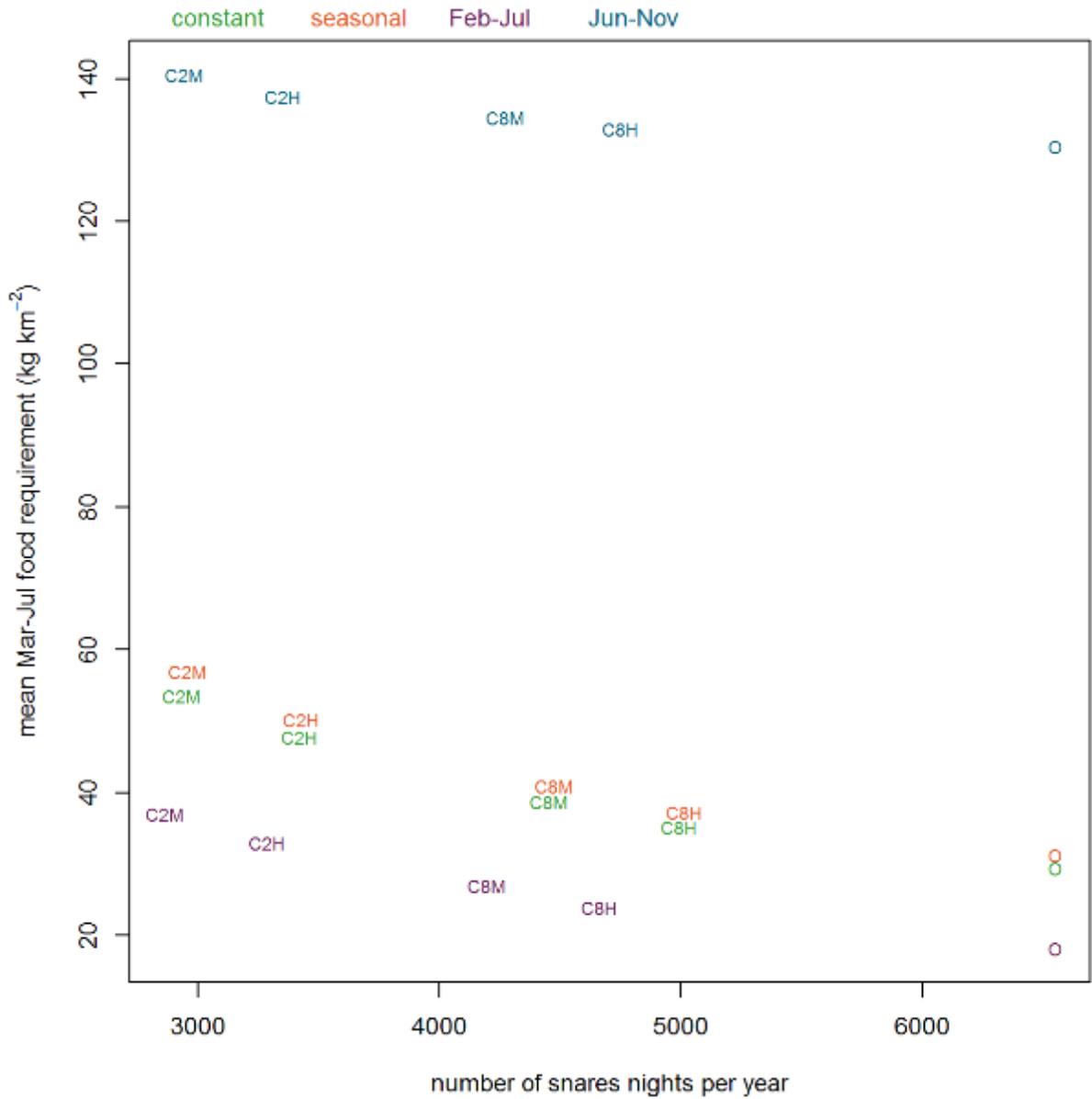


Figure 8.13. Trade-offs between nesting period food requirements and the number of snares used annually under open-loop (O) and closed-loop (C) MSE on the DLQ estate. For closed-loop options, numbers 2 or 8 refer to the number of search hours per week, letters M or H refer to the probability of finding scats if present (Medium = 0.5, High = 0.8). Results are shown under the maximum levels of effort for all methods.

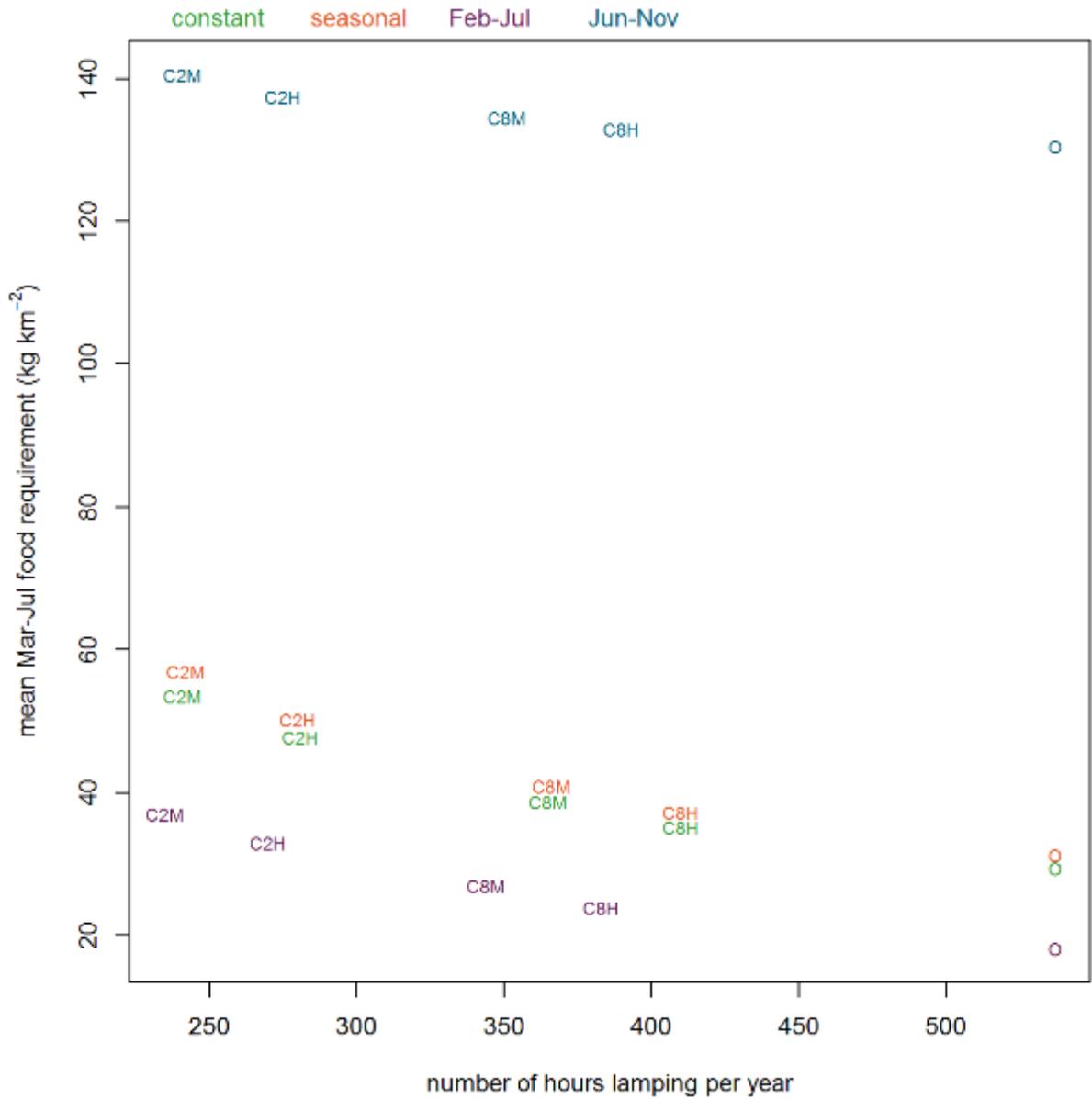


Figure 8.14. Trade-offs between nesting period food requirements and the number of lamping hours used annually under open-loop (O) and closed-loop (C) MSE on the DLQ estate. For closed-loop options, numbers 2 or 8 refer to the number of search hours per week, letters M or H refer to the probability of finding scats if present (Medium = 0.5, High = 0.8). Results are shown under the maximum levels of effort for all methods.

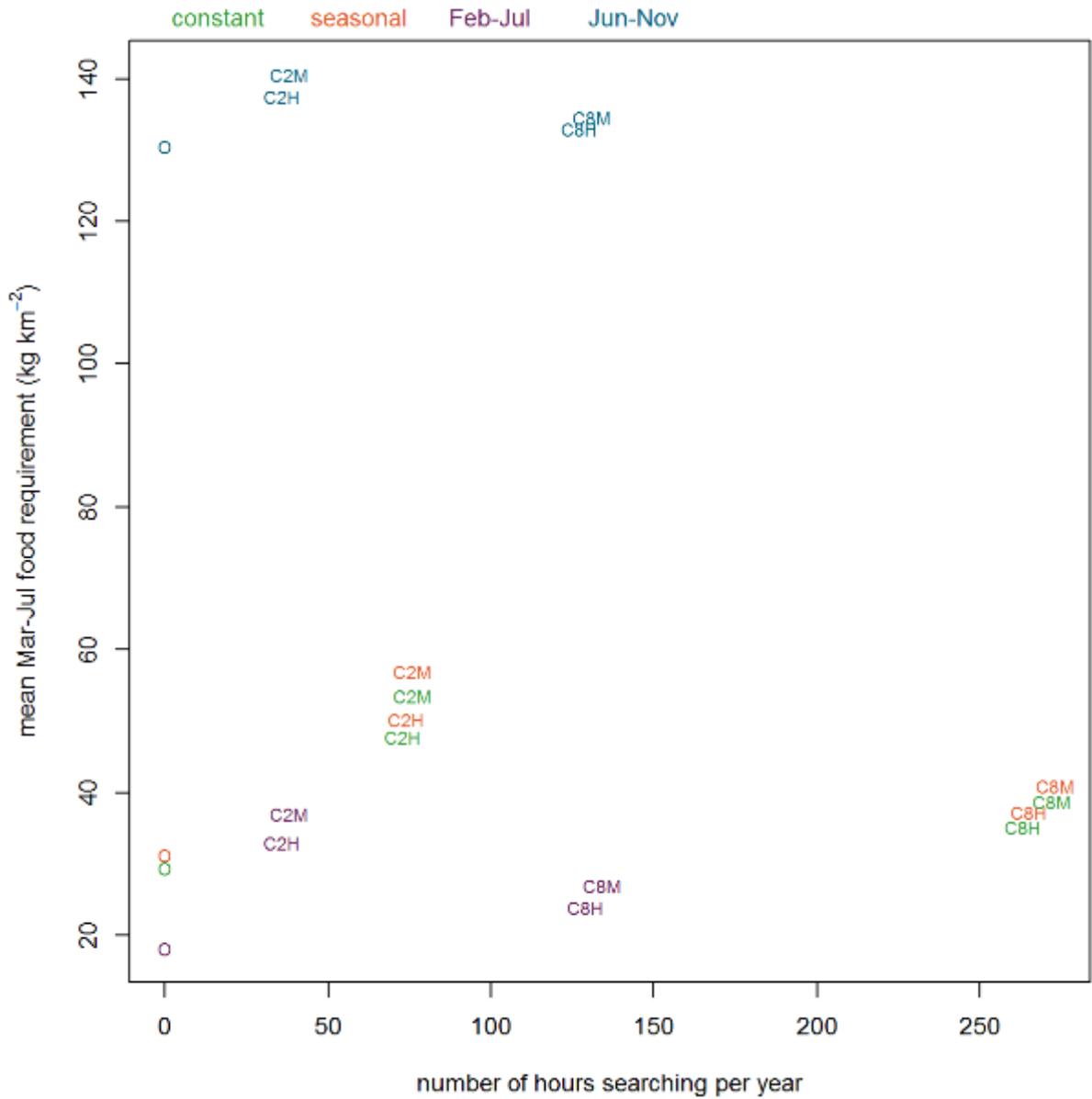


Figure 8.15. Trade-offs between nesting period food requirements and the number of hours spent searching for scats annually under open-loop (O) and closed-loop (C) MSE on the DLQ estate. For closed-loop options, numbers 2 or 8 refer to the number of search hours per week, letters M or H refer to the probability of finding scats if present (Medium = 0.5, High = 0.8). Results are shown under the maximum levels of effort for all methods.

Chapter 9: Conclusions

Many pest and predator control issues centre around reducing conflicts with prey species at local scales, because that is the scale at which management decisions are made. This is often achieved through the use of lethal methods, but the value of lethal control as a wildlife management tool is hotly debated. Until now, with notable exceptions such as American mink control (Porteus *et al.* 2012; Reynolds *et al.* 2013), it has been impossible to evaluate the effectiveness of predator control on restricted areas except through costly field experiments. Predator removal studies have demonstrated that fox control on restricted areas in Britain can reduce fox density and achieve positive effects on game and other ground-nesting bird species (Tapper, Potts & Brockless 1996; Stoate & Leake 2002; Fletcher *et al.* 2010; Potts 2012). Success at these sites was achieved by the annual removal of 2-3 foxes per km², but these studies represent a limited set of local circumstances and thus form a poor basis for generalisation to other restricted areas, i.e., shooting estates. National Gamebag Census data on annual fox bags suggested that many estates achieved or exceeded this level of culling, thereby indicating potential effective control. A fox bag of this size is, however, comparable only to the numbers of cubs produced annually, meaning that larger bags are explainable only by immigration. For bags smaller than this, it was unknown whether immigration was occurring or if control was effective at suppressing the fox population in any way. Replacement of culled animals is expected to occur on some time-scale, but raises the question of whether fox control is worthwhile in these situations. This can only be answered by understanding how local fox density changes in response to culling effort.

Most of the processes that determine the local density of foxes in restricted area culling – such as immigration rate and non-culling mortality – were previously unquantified even in broad terms. Foxes are difficult animals to work on, and the conventional field methods of wildlife biologists were not suitable to determine what was happening on in the fast-changing circumstances of intensive culling: in effect biologists could have to compete at a disadvantage of those doing the culling. The methods developed and described in this thesis use data recorded throughout the year as part of the culling process itself to obtain estimates of model parameters describing the key population processes. By modelling these

data on short time-steps this is the first time it has been possible to understand what was happening during the fox control operations, and evaluate how culling effort might have been used differently to better effect.

Datasets for individual estates in which lamping effort and number of sighted foxes were recorded daily (Fox Monitoring Scheme data) made it possible to develop an open-population depletion model incorporating the key processes that determine fox density on a restricted area. The simulation-estimation analysis showed that by fitting the fox model within a Bayesian state-space framework, reliable estimation of these parameters and reconstruction of fox density was possible on a weekly or two-weekly time-step given sufficient data. The minimum data requirements were for a time series covering three cub recruitment periods in each of which there were at least two weeks with lamping effort. The time series must also contain a minimum of eight weeks with lamping effort per year with no gap longer than nine months. Less than one third of the estates contributing to the FMS met these minimum data requirements. This highlighted the difficulties in obtaining informative data, but also shows that there are at least some gamekeepers sufficiently motivated to meet these data requirements. It is unknown whether more contributors to the FMS would have met the minimum data requirements had these been known beforehand.

Simulation-estimation analysis showed that a Bayesian estimation method that used informative prior probability distributions (i.e., priors) was necessary for reliable estimation of parameters using the fox model, although reconstructed fox density was on average within 10% of true values when vague priors were used. Priors were constructed for immigration rate, ν , instantaneous non-culling mortality rate M , *per capita* birth rate, r , and rate of successful search, d . The method to estimate ν using data from annual fox culling records resulted in the first known estimates of the rate of immigration into culled populations of foxes. The alternative methods of constructing an informative prior would have been to estimate immigration rate using capture-recapture modelling or within an integrated population model, both of which require expensive tagging-based field methods that are not viable in culled populations. The landscape-level estimates of ν showed the expected positive relationship with fox density, but also a positive relationship with the density of

released pheasants on estates within each landscape type. This suggested that increased prey availability through gamebird releasing was increasing the rate of replacement of culled foxes onto estates via immigration.

To date there are relatively few applications of Bayesian state-space modelling of animal population dynamics in terrestrial systems compared to marine and freshwater systems. This thesis is the first known application to fox populations. Intuitively, animal populations in terrestrial systems are subject to comparatively higher levels of process variability because the environment is less stable and human actions cause additional variability. A literature search of terrestrial studies supported this hypothesis as mean estimates of standard deviation in annual process errors σ_p larger than 0.2 were not uncommon. In this model, process errors were incorporated on short time-steps to allow for exceptional immigration events within one time-step, such as family groups moving onto an estate. Simulation-estimation analysis showed that the fox model generally allowed the estimation of the process errors in addition to observation errors, but that σ_p was only weakly identifiable. Because of this and due to moderate posterior correlations of other parameters with σ_p , the decision was made to fix σ_p for a two-week time step at 0.2 for use of the estimation model with real data from the FMS. This decision was supported by sensitivity analysis.

Fitting the fox model to data from FMS estates that met the minimum requirements enabled the impact of fox control efforts on fox density within these estates to be directly evaluated. This is the first time a credible evaluation of this kind has been possible. The reconstruction of fox density, as determined by the posterior median, showed that most estates achieved some level of suppression of the fox population relative to carrying capacity K , indicating that fox control was having an effect. However, few estates achieved consistently low fox densities, and although the lower credible intervals for fox density on some estates did include zero density, this was not for periods longer than three months during the nesting period. The actual objective of fox control on each of these modelled estates was not known. If the aim was to reduce fox density during the nesting period, i.e. when game and ground-nesting bird species are vulnerable to predation, the density estimates

from these estates during the nesting period suggest that improvements to fox control strategy could be made on most estates. The results from estate DLQ – where supplementary prey count data were available (Stoate & Leake 2002) – showed although on average through the year fox density was reduced only to about 50% of K , use of a strategy that focused control effort into the spring could be very effective at both reducing fox density at this time of year and increasing prey numbers in the autumn. As expected, the size of the fox bag on the majority of modelled estates was an unreliable indicator of culling effectiveness, e.g., use of the rule-of-thumb would have concluded that fox control on estate VAR was relatively ineffective with an annual fox bag of $1.83 \text{ fox km}^{-2} \text{ yr}^{-1}$, but the model revealed that fox density on this estate was actually heavily suppressed.

Posterior estimates of ν from FMS estates were generally high relative to the prior distribution. Fox density was suppressed on all estates to varying extents, but the rate at which immigration appeared to replace culled foxes indicated that fox control on these estates was more challenging than might have been expected. These results support previous empirical studies by suggesting that these shooting estates were fox population sinks as a result of control, not sources as a result of high prey density. All parameter estimates were generally similar whether it was assumed that immigration was a constant process throughout the year or was seasonal during the fox dispersal period. The estimates for the *per capita* birth rate, r , and the instantaneous rate of non-culling mortality, M , were the most sensitive to the choice of prior used for them. For M this was not unexpected as the simulation-estimation analysis had shown that the parameter was only weakly identifiable. Nevertheless, the reconstructed fox density was not affected by the choice of prior for r and M . Given these estimates of M , non-culling mortality risk appears to be a relatively small but not insignificant factor in total fox mortality for culled fox populations on restricted areas.

It was expected that there would be some large-scale spatial patterns in parameter estimates due to landscape or regional effects that would make the use of a spatial hierarchical Bayesian model suitable, but there were unexpectedly high levels of variation in parameter estimates between FMS estates that were close to one another, particularly for ν and K . This is unlikely to be an artefact of, e.g., imprecise data and indeterminacy since the

marginal posterior estimates of these parameters were quite precise and the posterior correlations were fairly small in magnitude. Few estates in the FMS also contributed to the NGC, but those that did allowed an analysis that related estimates of these parameters to data on gamebird releasing from the NGC. These results suggested that gamebird releasing increased the carrying capacity of the estate for foxes, attracted an increased rate of immigration to replace culled foxes, and possibly also increased cub production. These conclusions are based upon only five data points (estates) and so must be treated with appropriate caution, but add evidence to the landscape-scale relationship found between immigration rate and gamebird release density. Importantly, it appears that the effect of gamebird releasing on within-estate fox density was not counteracted by effective fox control, as those estates releasing more gamebirds had both higher fox densities and put less effort into fox control, compared with estates managing for wild gamebirds. With the increasing trend in gamebird releasing in Britain showing little sign of slowing (Aebischer 2013), the impact of higher fox densities could have serious negative consequences on more vulnerable species that are impacted by fox predation.

The posterior probability distributions estimated from these estates are now available to be used as priors in an updated model when new data are collected. Such an iterative approach to analysis is one of the advantages of Bayesian methods and should lead to increased precision in future parameter estimates. Another use of the joint posterior is to parameterise operating models in a management strategy evaluation (MSE). While MSE has recently been applied to vertebrate pest control issues (e.g. Western grey kangaroo, Chee & Wintle 2010), this thesis presents a new application of MSE modelling to understand fox control issues. The MSE analyses provided useful insights into the relative effectiveness of different culling methods. Whether lamping only or snaring only was the more effective method varied between estates, but in contrast the removal of cubs (only) at earths was not found to be effective on any estate. This would suggest that restriction of the methods allowed to kill cubs at earths, as happened under the Hunting Act (2004), potentially had only a limited impact on the success of culling, provided that the adult foxes were removed elsewhere on an estate. The MSE analyses also showed that a change of policy imposing seasonal restrictions on the use of culling methods during certain times of year, e.g. spring,

would have consequences for the predation pressure experienced by game and ground-nesting bird populations.

Concentrating fox control effort into spring-summer (referred to as ‘spring-only’ control) was found to be the most effective strategy with respect to the objective of minimising bird nesting period food requirements on all estates. This strategy is similar to that applied on estate DLQ during the FMS, with documented positive effects for wild game species. Autumn-only fox control was consistently the least effective strategy at minimising nesting period food requirements. However, as a summer-autumn control strategy (referred to as ‘autumn-only’ control) is more likely to be applied on a released bird estate it might be better evaluated against an objective that aimed to reduce potential fox predation during the release period. The high food requirement of fox populations during the nesting period under an autumn-only control strategy suggests that breeding numbers and productivity of wild birds is likely to be poor where this strategy is applied. This leads to a potentially important indirect effect of the autumn-only strategy. A typical response to poor productivity would be to release an increased number of birds onto the estate to ensure that it is possible to run a shoot the following season. Accordingly, less effort might then be available for fox control, leading to increased fox predation, more releasing, and so on.

Strategies in which culling effort was spread throughout the year were less effective than spring-only fox control at reducing the nesting period food requirements. An advantage of adopting a year-round approach was, however, that food requirements of the fox population were kept at lower levels during the autumn and winter when compared to spring-only control. Where management is for a species with poor over-winter survival, e.g., grey partridge (Potts 2012), less effective fox control and a reduction in breeding success through application of a year-round control strategy to ensure that enough adults survived to nesting time might be a necessary trade-off. A disadvantage of a year-round control strategy is that by removing foxes throughout the year the potential for fox predation to control other pest species on an estate, e.g., rabbits or rats, is reduced, thereby increasing the cost to the gamekeeper of performing these actions instead.

Closed-loop MSE modelling revealed a number of further trade-offs that a gamekeeper faces when making decisions on fox control strategy. Here the trade-off is between the ability to perform effective control and potential efficiency and welfare costs. The use of scat searching effort to target culling effort achieved only slightly less effective fox control than naïve use of effort, but involved considerably less snaring and lamping effort. Although small, the difference in impact between targeted and naïve culling effort it might be critical for a small or vulnerable population of game. In these instances gamekeepers are most likely to adopt a precautionary option and use maximum culling effort regardless of feedback (i.e. open-loop). Both spring and year-round control lead to trade-offs between ability to perform effective control and humaneness because they require culling during the fox breeding season, potentially orphaning dependent cubs. This welfare cost could lead directly to political change and reduced options for fox control during the spring. It is now clear that this would limit the effectiveness of fox control aimed to benefit wild prey species.

9.1 Future directions

One of the main outcomes from this thesis was that management advice on culling strategy would differ among estates, dependent on local circumstances. Estate-specific parameter estimates derived from the FMS could be used as the basis for advice, but only if conditions on the estate remain as they were when the data were recorded. As it dates from the period 1996-2000, the FMS dataset is now over 15 years old, and circumstances on many of the estates represented will have changed.

One major change is that the methods legally available to control foxes have been restricted through the Hunting Act 2004; this prevents the use of terrier dogs to kill cubs at breeding earths, although they may still be shot once old enough to emerge above ground. (The use of fumigants became illegal prior to the FMS.) There have also been technological improvements to snaring hardware (Short *et al.* 2012); and to night-shooting equipment with the increased availability of night-vision binoculars and rifle scopes. The increasing trend in gamebird release density during the intervening years may also mean that the factors determining fox density have changed, if not on these estates then on neighbouring estates.

In order to better understand the current situation it would be necessary to repeat the Fox Monitoring Scheme and collect data over a minimum three year period.

Several improvements could be made to the FMS if it were to be repeated. Obtaining data from estates that are more representative of the range of conditions in Britain, e.g., by stratifying by region or landscape, would be an important step. Upland estates managed for grouse shooting were notably under-represented in the original FMS in comparison to lowland estates managed for pheasant and partridge. There are gamekeepers who are sufficiently motivated to record the required data but it would probably require considerable effort to recruit estates in these under-represented areas (i.e. northern England, Wales and Scotland). To maximise the information content of future data, deliberate variation in control strategy between and within estates over a multi-year period would be useful to result in more informative data for modelling. Convincing gamekeepers and estate owners that this would be necessary could be challenging, particularly where reduced fox control effort might compromise the ability to produce enough wild game to successfully run a shoot on an estate.

Additional information on the sighting process could improve future estimates. Alternative lamping methods, e.g. from a vehicle or on foot and with or without night-vision equipment, may affect different component parameters of the rate of successful search, i.e. search rate and sighting probability. Estimates of the rate of successful search could therefore become more accurate through use of alternative priors appropriate to the exact method used. Knowledge of seasonal variation in sighting probability would also help in this regard. The economic cost of alternative culling strategies was not considered in this thesis as the cost of effort for each method was not comparable. Data on snare usage and time spent on snare maintenance together with time spent using other methods, e.g., at earths to remove cubs, would add value to a future dataset. With this information trade-offs between effective control and economic cost could be better explored. Data on prey availability, e.g., gamebird release densities or autumn game counts would also add value. This would enable a more complete analysis of the relationships between parameter estimates and prey availability to potentially answer the questions raised here about how gamebird releasing impacts fox populations.

9.2 Concluding remarks

The effectiveness of fox control on restricted areas is difficult to evaluate but the justification of lethal control will increasingly be required (Fall & Jackson 2002). Any evaluation of fox control must be performed at the local scale as differences between areas in the population processes that determine fox density mean that generalisations can be very misleading. This thesis provides a modelling approach that can be used to evaluate the within-year effect of past fox control and determine the likely effect of future control strategy. These methods go some way towards being able to regularly evaluate individual culling efforts, with iterative Bayesian updating offering to improve the understanding of population processes at the local scale. A fairly substantial amount of data are required to fit the fox model and so the challenge remains for gamekeepers to collect these data as part of their normal culling operations, rather than as a part of extensive surveys managed by external organisations. Modern technology, e.g., smartphone applications, could help with this data recording in the future. There may even come a time when the fitting of models such as this becomes automated on the computing cloud, allowing gamekeepers to evaluate their culling effort in real-time. This novel approach to evaluating fox control can be extended to other pest and predator control issues provided that its rather strict requirements are met, e.g., the availability of suitable data and construction of informative prior probability distributions for model parameters for the system in question.

References

- Abadi, F., Gimenez, O., Arlettaz, R. & Schaub, M. (2010a) An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. *Ecology*, **91**, 7–14.
- Abadi, F., Gimenez, O., Ullrich, B., Arlettaz, R. & Schaub, M. (2010b) Estimation of immigration rate using integrated population models. *Journal of Applied Ecology*, **47**, 393–400.
- Aebischer, N. (2013) National Gamebag Census: released game species. *Game & Wildlife Conservation Trust Review*, **44**, 34–37.
- Aebischer, N.J., Davey, P.D. & Kingdon, N.G. (2011) *National Gamebag Census: Mammal Trends to 2009*. Game & Wildlife Conservation Trust, Fordingbridge, UK.
- Aebischer, N.J., Robertson, P.A. & Kenward, R.E. (1993) Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, **74**, 1313–1325.
- Ahrestani, F.S., Hebblewhite, M. & Post, E. (2013) The importance of observation versus process error in analyses of global ungulate populations. *Scientific Reports*, **3**.
- Aitchison, J. (1986) *The Statistical Analysis of Compositional Data*. Chapman and Hall, London, UK.
- Allen, S.H. (1983) Comparison of red fox litter sizes determined from counts of embryos and placental scars. *The Journal of Wildlife Management*, **47**, 860–863.
- Angelstam, P., Lindström, E. & Widén, P. (1984) Role of Predation in Short-Term Population Fluctuations of Some Birds and Mammals in Fennoscandia. *Oecologia*, **62**, 199–208.
- Angelstam, P., Lindström, E. & Widén, P. (1985) Synchronous Short-Term Population Fluctuations of Some Birds and Mammals in Fennoscandia: Occurrence and Distribution. *Holarctic Ecology*, **8**, 285–298.
- Anon. (1999) The Allerton Project. *Game Conservancy Trust Review*, **30**, 54–60.
- Arreguín-Sánchez, F. (1996) Catchability: a key parameter for fish stock assessment. *Reviews in Fish Biology and Fisheries*, **6**, 221–242.
- Arroyo, B. & Beja, P. (2002) *Impact of Hunting Management Practices on Biodiversity - Final Report of the Workpackage 2 of the Project Reconciling Gamebird Hunting and Biodiversity (REGHAB)*. Institute of Terrestrial Ecology and Instituto de Investigacion en Recursos Cinergeticos.

- Bacon, P.J. (1985) Discrete time temporal models of rabies. *Population Dynamics of Rabies in Wildlife* (ed P.J. Bacon), pp. 147–196. Academic Press, London, UK.
- Baker, P.J., Dowding, C.V., Molony, S.E., White, P.C.L. & Harris, S. (2007) Activity patterns of urban red foxes (*Vulpes vulpes*) reduce the risk of traffic-induced mortality. *Behavioral Ecology*, **18**, 716–724.
- Baker, P.J., Funk, S.M., Harris, S. & White, P.C.L. (2000) Flexible spatial organization of urban foxes, *Vulpes vulpes*, before and during an outbreak of sarcoptic mange. *Animal Behaviour*, **59**, 127–146.
- Baker, P.J., Furlong, M., Southern, S. & Harris, S. (2006) The potential impact of red fox *Vulpes vulpes* predation in agricultural landscapes in lowland Britain. *Wildlife Biology*, **12**, 39–50.
- Baker, P.J. & Harris, S. (2003) A review of the diet of foxes in rural Britain and a preliminary assessment of their impact as a predator. *Conservation & Conflict: Mammals & Farming in Britain* Linnaean Society Occasional Publication. (eds F. Tattersall & W. Manley), pp. 120–140. Westbury Publishing, Otley, Yorkshire, UK.
- Baker, P.J. & Harris, S. (2006) Does culling reduce fox (*Vulpes vulpes*) density in commercial forests in Wales, UK? *European Journal of Wildlife Research*, **52**, 99–108.
- Baker, P.J. & Harris, S. (2008) The fox. *Mammals of the British Isles: Handbook*, 4th ed (eds S. Harris & D.W. Yalden), pp. 407–423. The Mammal Society, Southampton, UK.
- Baker, P.J., Harris, S., Robertson, C.P.J., Saunders, G. & White, P.C.L. (2001) Differences in the capture rate of cage-trapped red foxes *Vulpes vulpes* and an evaluation of rabies control measures in Britain. *Journal of Applied Ecology*, **38**, 823–835.
- Bakken, M. (1993a) Reproduction in farmed silver fox vixens, *Vulpes vulpes*, in relation to own competition capacity and that of neighbouring vixens. *Journal of Animal Breeding and Genetics*, **110**, 305–311.
- Bakken, M. (1993b) The relationship between competition capacity and reproduction in farmed silver-fox vixens, *Vulpes vulpes*. *Journal of Animal Breeding and Genetics*, **110**, 147–155.
- Bangs, E.E., Bailey, T.N. & Portner, M.F. (1989) Survival rates of adult female moose on the Kenai Peninsula, Alaska. *Journal of Wildlife Management*, **53**, 557–563.
- Barr, C.J. (1998) *The Sampling Strategy for Countryside Survey 2000*. Department of the Environment, Transport and the Regions.
- Barthelmeß, E. & Brooks, M. (2010) The influence of body-size and diet on road-kill trends in mammals. *Biodiversity and Conservation*, **19**, 1611–1629.

- Battersby, J. (2005) *UK Mammals: Species Status and Population Trends*. JNCC/Tracking Mammals Partnership, Peterborough, UK.
- Besbeas, P., Freeman, S.N., Morgan, B.J.T. & Catchpole, E.A. (2002) Integrating Mark-Recapture-Recovery and Census Data to Estimate Animal Abundance and Demographic Parameters. *Biometrics*, **58**, 540–547.
- Beverton, R.J.H. (1963) Maturation, growth and mortality of Clupeid and Engraulid stocks in relation to fishing. *Rapports et procès-verbaux réunions, Conseil International pour l'Exploration de la Mer*, **154**, 44–67.
- Beverton, R.J.H. & Holt, S.J. (1959) A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. *The Lifespan of Animals* CIBA Foundation Colloquium on Aging. pp. 142–180. Churchill, London, UK.
- Bischof, R., Hameed, S., Ali, H., Kabir, M., Younas, M., Shah, K.A., Din, J.U. & Nawaz, M.A. (2014) Using time-to-event analysis to complement hierarchical methods when assessing determinants of photographic detectability during camera trapping. *Methods in Ecology and Evolution*, **5**, 44–53.
- Bischof, R., Nilsen, E.B., Brøseth, H., Männil, P., Ozoliņš, J. & Linnell, J.D.C. (2012) Implementation uncertainty when using recreational hunting to manage carnivores. *Journal of Applied Ecology*, **49**, 824–832.
- Boatman, N.D. & Brockless, M.H. (1998) The Allerton Project: farmland management for partridges (*Perdix perdix*, *Alectoris rufa*) and pheasants (*Phasianus colchicus*). *Gibier Faune Sauvage*, **15**, 563–574.
- Bolker, B.M. (2008) *Ecological Models and Data in R*. Princeton University Press, Princeton, NJ, USA.
- Brett, M.T. (2004) When is a correlation between non-independent variables ‘spurious’? *Oikos*, **105**, 647–656.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.
- Bryan, M.D. (2012) *Management Procedure Evaluation of a Data-Limited Multispecies Fishery with Application to the Hawaiian Bottomfish Fishery*. Ph.D, University of British Columbia, Vancouver.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK.
- Buckland, S.T., Newman, K.B., Fernández, C., Thomas, L. & Harwood, J. (2007) Embedding population dynamics models in inference. *Statistical Science*, **22**, 44–58.

- Bucknell, R. (2001) *Foxing with Lamp and Rifle*. Foxearth Publishing, Chelmsford, UK.
- Bunce, R.G.H., Barr, C.J., Clarke, R.T., Howard, D.C. & Lane, A.M.J. (1996a) Land classification for strategic ecological survey. *Journal of Environmental Management*, **47**, 37–60.
- Bunce, R.G.H., Barr, C.J., Clarke, R.T., Howard, D.C. & Lane, A.M.J. (1996b) ITE Merlewood Land Classification of Great Britain. *Journal of Biogeography*, **23**, 625–634.
- Bunce, R.G.H., Barr, C.J. & Whittaker, H.A. (1981) *Land Classes in Great Britain: Preliminary Descriptions for Users of the Merlewood Method of Land Classification*. Institute of Terrestrial Ecology.
- Bunnefeld, N., Hoshino, E. & Milner-Gulland, E.J. (2011) Management strategy evaluation: a powerful tool for conservation? *Trends in Ecology & Evolution*, **26**, 441–447.
- Butterworth, D.S. & Punt, A.E. (1999) Experiences in the evaluation and implementation of management procedures. *ICES Journal of Marine Science*, **56**, 985–998.
- Calder, W.A. (1984) *Size, Function and Life History*. Harvard University Press, Cambridge, MA, USA.
- Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.
- Carey, J.R. & Judge, D.S. (2000) *Longevity Records: Life Spans of Mammals, Birds, Amphibians, Reptiles, and Fish*. Odense University Press, Odense, Denmark.
- Case, T.J. (2000) *An Illustrated Guide to Theoretical Ecology*. Oxford University Press, Oxford, UK.
- Caughley, G. (1977) *Analysis of Vertebrate Populations*. John Wiley & Sons, New York, NY, USA.
- Cavallini, P. & Lovari, S. (1991) Environmental factors influencing the use of habitat in the red fox, *Vulpes vulpes*. *Journal of Zoology*, **223**, 323–339.
- Cavallini, P. & Santini, S. (1996) Reproduction of the red fox *Vulpes vulpes* in Central Italy. *Annales Zoologici Fennici*, **33**, 267–274.
- CEH. (2005) *Countryside Information System, Version 8.0*. Centre for Ecology & Hydrology, Bailrigg, UK.
- Charnov, E.L. (1993) *Life History Invariants*. Oxford University Press, Oxford, UK.
- Chee, Y.E. & Wintle, B.A. (2010) Linking modelling, monitoring and management: an integrated approach to controlling overabundant wildlife. *Journal of Applied Ecology*, **47**,

1169–1178.

Choquenot, D., Hone, J. & Saunders, G. (1999) Using aspects of predator-prey theory to evaluate helicopter shooting for feral pig control. *Wildlife Research*, **26**, 251–261.

Clark, W.G. (1999) Effects of an erroneous natural mortality rate on a simple age-structured stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1721–1731.

Clark, J.S. (2005) Why environmental scientists are becoming Bayesians. *Ecology Letters*, **8**, 2–14.

Clark, F., Brook, B.W., Delean, S., Reşit Akçakaya, H. & Bradshaw, C.J.A. (2010) The theta-logistic is unreliable for modelling most census data. *Methods in Ecology and Evolution*, **1**, 253–262.

Cook, T.C. & Blumstein, D.T. (2013) The omnivore's dilemma: Diet explains variation in vulnerability to vehicle collision mortality. *Biological Conservation*, **167**, 310–315.

Côté, I.M. & Sutherland, W.J. (1997) The effectiveness of removing predators to protect bird populations. *Conservation Biology*, **11**, 395–405.

Coulson, J.C. & Fairweather, J.A. (2001) Reduced reproductive performance prior to death in the Black-legged Kittiwake: senescence or terminal illness? *Journal of Avian Biology*, **32**, 146–152.

Craig, P.S. (2003) *Echinococcus multilocularis*. *Current Opinion in Infectious Diseases*, **16**, 437–444.

Cressie, N., Calder, C.A., Clark, J.S., van Hoef, J.M. & Wikle, C.K. (2009) Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. *Ecological Applications*, **19**, 553–570.

Davies, J.M., Roper, T.J. & Shepherdson, D.J. (1987) Seasonal distribution of road kills in the European badger (*Meles meles*). *Journal of Zoology*, **211**, 525–529.

Van Deelen, T. & Etter, D. (2003) Effort and the functional response of deer hunters. *Human Dimensions of Wildlife*, **8**, 97–108.

Defra. (2005) *Defra Code of Practice on the Use of Snares in Fox and Rabbit Control*. Department for Environment, Food and Rural Affairs, London, UK.

Defra. (2012) *Determining the Extent of Use and Humaneness of Snares in England and Wales. Report Submitted to Defra*.

DeLury, D.B. (1947) On the estimation of biological populations. *Biometrics*, **3**, 145–167.

Dennis, B. (1996) Should ecologists become Bayesians? *Ecological Applications*, **6**, 1095–

1103.

Deriso, R.B., Quinn, T.J. & Neal, P.R. (1985) Catch-age analysis with auxiliary information. *Canadian Journal of Fisheries and Aquatic Sciences*, **42**, 815–824.

Devenish-Nelson, E.S., Harris, S., Soulsbury, C.D., Richards, S.A. & Stephens, P.A. (2013) Demography of a carnivore, the red fox, *Vulpes vulpes*: what have we learnt from 70 years of published studies? *Oikos*, **122**, 705–716.

Dodds, P.S., Rothman, D.H. & Weitz, J.S. (2001) Re-examination of the ‘3/4-law’ of metabolism. *Journal of Theoretical Biology*, **209**, 9–27.

Doncaster, C.P. & Macdonald, D.W. (1991) Drifting territoriality in the red fox *Vulpes vulpes*. *Journal of Animal Ecology*, **60**, 423–439.

Dorazio, R.M. & Johnson, F.A. (2003) Bayesian inference and decision theory - a framework for decision making in natural resource management. *Ecological Applications*, **13**, 556–563.

Downing, R.L. (1980) Vital statistics of animal populations. *Wildlife Techniques Manual* pp. 247–267. The Wildlife Society, Washington, DC, USA.

Draycott, R.A.H., Hoodless, A.N., Woodburn, M.I.A. & Sage, R.B. (2008) Nest predation of common pheasants *Phasianus colchicus*. *Ibis*, **150**, 37–44.

Eaton, M.A., Brown, A.F., Noble, D.G., Musgrove, A.J., Hearn, R.D., Aebischer, N.J., Gibbons, D.W., Evans, A.D. & Gregory, R.D. (2009) Birds of Conservation Concern 3: the population status of birds in the United Kingdom, Channel Islands and Isle of Man. *British Birds*, **102**, 296–341.

Edgington, E.S. (1995) *Randomization Tests*, 3rd ed. Marcel Dekker, Inc., New York, NY, USA.

Edwards, C.T.T., Bunnfeld, N., Balme, G.A. & Milner-Gulland, E.J. (2014) Data-poor management of African lion hunting using a relative index of abundance. *Proceedings of the National Academy of Sciences*, **111**, 539–543.

Ellison, A.M. (1996) An introduction to Bayesian inference for ecological research and environmental decision making. *Ecological Applications*, **6**, 1036–1046.

Ellison, A.M. (2004) Bayesian inference in ecology. *Ecology Letters*, **7**, 509–520.

Endler, J.A. (1991) Interactions between predators and prey. *Behavioural Ecology: An Evolutionary Approach* (eds J.R. Krebs & N.B. Davies), pp. 169–196. Blackwell Scientific, Oxford, UK.

Englund, J. (1970) Some aspects of reproduction and mortality rates in Swedish foxes (*Vulpes vulpes*), 1961–63 and 1966–69. *Viltrevy*, **8**, 1–82.

Evans, M., Hastings, N.A.J. & Peacock, J.B. (2000) *Statistical Distributions*, 3rd ed. Wiley, New York, NY, USA.

Ewald, J.A., Potts, G.R. & Aebischer, N.J. (2012) Restoration of a wild grey partridge shoot: a major development in the Sussex study, UK. *Animal Biodiversity and Conservation*, **35**, 363–369.

Fahrig, L. & Rytwinski, T. (2009) Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society*, **14**, 21.

Fall, M.W. & Jackson, W.B. (2002) The tools and techniques of wildlife damage management—changing needs: an introduction. *International Biodeterioration & Biodegradation*, **49**, 87–91.

Fewster, R.M., Southwell, C., Borchers, D.L., Buckland, S.T. & Pople, A.R. (2008) The influence of animal mobility on the assumption of uniform distances in aerial line-transect surveys. *Wildlife Research*, **35**, 275–288.

Field, S.A., Tyre, A.J., Thorn, K.H., O'Connor, P.J. & Possingham, H.P. (2005) Improving the efficiency of wildlife monitoring by estimating detectability: a case study of foxes (*Vulpes vulpes*) on the Eyre Peninsula, South Australia. *Wildlife Research*, **32**, 253–258.

Fletcher, K., Aebischer, N.J., Baines, D., Foster, R. & Hoodless, A.N. (2010) Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *Journal of Applied Ecology*, **47**, 263–272.

Ford, A.T. & Fahrig, L. (2007) Diet and body size of North American mammal road mortalities. *Transportation Research Part D*, **12**, 498–505.

Frain, S. (2006) *Fox Control*. Swan Hill Press, Shrewsbury, UK.

Fryxell, J.M., Mercer, W.E. & Gellately, R.B. (1988) Population dynamics of Newfoundland moose using cohort analysis. *The Journal of Wildlife Management*, **52**, 14–21.

Fujii, K., Holling, C. & Mace, P. (1986) A simple generalized model of attack by predators and parasites. *Ecological Research*, **1**, 141–156.

Gaillard, J.-M., Viallefont, A., Loison, A. & Festa-Bianchet, M. (2004) Assessing senescence patterns in populations of large mammals. *Animal Biodiversity and Conservation*, **27**, 47–58.

Garrard, G.E., Bekessy, S.A., McCarthy, M.A. & Wintle, B.A. (2008) When have we looked hard enough? A novel method for setting minimum survey effort protocols for flora surveys. *Austral Ecology*, **33**, 986–998.

Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (2004) *Bayesian Data Analysis*, 2nd ed. Chapman & Hall, London, UK.

- Gelman, A. & Hill, J. (2007) *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York, NY, USA.
- Gendron, R.P. & Staddon, J.E.R. (1983) Searching for cryptic prey: the effect of search rate. *The American Naturalist*, **121**, 172–186.
- Gese, E.M. (2001) Monitoring of terrestrial carnivore populations. *Carnivore Conservation* (eds J.L. Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), pp. 372–396. Cambridge University Press & The Royal Zoological Society of London, Cambridge, UK.
- Geweke, J. (1992) Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. *Bayesian Statistics 4* (eds J.M. Bernardo, J. Berger, A.P. Dawid & A.F.M. Smith), pp. 169–193. Oxford University Press, Oxford, UK.
- Gilpin, M.E. & Ayala, F.J. (1973) Global models of growth and competition. *Proceedings of the National Academy of Sciences*, **70**, 3590–3593.
- Gimenez, O., Bonner, S.J., King, R., Parker, R.A., Brooks, S.P., Jamieson, L.E., Grosbois, V., Morgan, B.J.T. & Thomas, L. (2009) WinBUGS for population ecologists: Bayesian modeling using Markov Chain Monte Carlo methods. *Modeling Demographic Processes in Marked Populations* (eds D.L. Thomas, E.G. Cooch & M.J. Conroy), pp. 883–915. Springer, New York, NY, USA.
- Gimenez, O., Viallefont, A., Catchpole, E.A., Choquet, R. & Morgan, B.J.T. (2004) Methods for investigating parameter redundancy. *Animal Biodiversity and Conservation*, **27**, 561–572.
- Gislason, H. & Helgason, T. (1985) Species interaction in assessment of fish stocks with special application to the North Sea. *Dana*, **5**, 1–44.
- Goddard, H.N. & Reynolds, J.C. (1993) Age determination in the red fox (*Vulpes vulpes* L.) from tooth cementum lines. *Gibier Faune Sauvage*, **10**, 173–187.
- Grilo, C., Bissonette, J.A. & Santos-Reis, M. (2009) Spatial-temporal patterns in Mediterranean carnivore road casualties: Consequences for mitigation. *Biological Conservation*, **142**, 301–313.
- Groot Bruinderink, G.W.T.A. & Hazebroek, E. (1996) Ungulate traffic collisions in Europe. *Conservation Biology*, **10**, 1059–1067.
- Grue, H. & Jensen, B. (1979) Review of the formation of incremental lines in tooth cementum of terrestrial mammals. *Danish Review of Game Biology*, **11**, 1–48.
- Guilford, T. & Dawkins, M.S. (1987) Search images not proven: A reappraisal of recent evidence. *Animal Behaviour*, **35**, 1838–1845.
- Guthery, F.S. & Shaw, J.H. (2013) Density dependence: applications in wildlife management. *The Journal of Wildlife Management*, **77**, 33–38.

- Güthlin, D., Kröschel, M., Küchenhoff, H. & Storch, I. (2012) Faecal sampling along trails: a questionable standard for estimating red fox *Vulpes vulpes* abundance. *Wildlife Biology*, **18**, 374–382.
- Haines-Young, R., Barr, C.J., Firbank, L.G., Furse, M., Howard, D.C., McGowan, G., Petit, S., Smart, S.M. & Watkins, J.W. (2003) Changing landscapes, habitats and vegetation diversity across Great Britain. *Journal of Environmental Management*, **67**, 267–281.
- Halley, J. & Inchausti, P. (2002) Lognormality in ecological time series. *Oikos*, **99**, 518–530.
- Hall, N.G., Hesp, S.A. & Potter, I.C. (2004) A Bayesian approach for overcoming inconsistencies in mortality estimates using, as an example, data for *Acanthopagrus latus*. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 1202–1211.
- Harding, E.K., Doak, D.F. & Albertson, J.D. (2001) Evaluating the effectiveness of predator control: the non-native red fox as a case study. *Conservation Biology*, **15**, 1114–1122.
- Harris, S. (1977) Distribution, habitat utilization and age structure of a suburban fox (*Vulpes vulpes*) population. *Mammal Review*, **7**, 25–39.
- Harris, S. (1979) Age-related fertility and productivity in red foxes, *Vulpes vulpes*, in suburban London. *Journal of Zoology*, **187**, 195–199.
- Harris, S. (1980) Home ranges and patterns of distribution of foxes (*Vulpes vulpes*) in an urban area as revealed by radio tracking. *A handbook on biotelemetry and radio tracking* (eds C.J. Amlaner & D.W. Macdonald), pp. 685–690. Pergamon Press, Oxford, UK.
- Harris, S., Morris, P., Wray, S. & Yalden, D.W. (1995) *A Review of British Mammals: Population Estimates and Conservation Status of British Mammals Other than Cetaceans*. JNCC, Peterborough, UK.
- Harris, S. & Smith, G.C. (1987) Demography of two urban fox (*Vulpes vulpes*) populations. *Journal of Applied Ecology*, **24**, 75–86.
- Harris, S. & Trehwella, W.J. (1988) An analysis of some of the factors affecting dispersal in an urban fox (*Vulpes vulpes*) population. *Journal of Applied Ecology*, **25**, 409–422.
- Hartley, F.G.L., Follett, B.K., Harris, S., Hirst, D. & McNeilly, A.S. (1994) The endocrinology of gestation failure in foxes (*Vulpes vulpes*). *Journal of Reproduction and Fertility*, **100**, 341–346.
- Hassell, M.P. (1975) Density-dependence in single-species populations. *Journal of Animal Ecology*, **44**, 283–295.
- Henry, J.D. (1986) *Red Fox: The Catlike Canine*. Smithsonian Institution Press, Washington, DC, USA.

- Hewson, R. (1986) Distribution and density of fox breeding dens and the effects of management. *Journal of Applied Ecology*, **23**, 531–538.
- Heydon, M.J. & Reynolds, J.C. (2000a) Fox (*Vulpes vulpes*) management in three contrasting regions in Britain, in relation to agricultural and sporting interests. *Journal of Zoology*, **251**, 237–252.
- Heydon, M.J. & Reynolds, J.C. (2000b) Demography of rural foxes (*Vulpes vulpes*) in relation to cull intensity in three contrasting regions of Britain. *Journal of Zoology*, **251**, 265–276.
- Heydon, M.J., Reynolds, J.C. & Short, M.J. (2000) Variation in abundance of foxes (*Vulpes vulpes*) between three regions of rural Britain, in relation to landscape and other variables. *Journal of Zoology*, **251**, 253–264.
- Hilborn, R. (1979) Comparison of fisheries control systems that utilize catch and effort data. *Journal of the Fisheries Research Board of Canada*, **36**, 1477–1489.
- Hilborn, R. (2007) Managing fish is managing people: what has been learned? *Fish and Fisheries*, **8**, 285–296.
- Hilborn, R. & Liermann, M. (1998) Standing on the shoulders of giants: learning from experience in fisheries. *Reviews in Fish Biology and Fisheries*, **8**, 273–283.
- Hilborn, R. & Walters, C.J. (1992) *Quantitative Fisheries Stock Assessment: Choice, Dynamics & Uncertainty*. Chapman & Hall Inc., New York, NY, USA.
- Hoenig, J.M. (1982) *A Compilation of Mortality and Longevity Estimates for Fish, Molluscs, and Cetaceans, with a Bibliography of Comparative Life History Studies*. Graduate School of Oceanography, University of Rhode Island.
- Hoenig, J.M. (1983) Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin*, **82**, 898–903.
- Holling, C.S. (1959a) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, **91**, 385–398.
- Holling, C.S. (1959b) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist*, **91**, 293–320.
- Holling, C.S. (1965) The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada*, **97**, 5–60.
- Holmala, K. & Kauhala, K. (2006) Ecology of wildlife rabies in Europe. *Mammal Review*, **36**, 17–36.

- Holt, A.R., Davies, Z.G., Tyler, C. & Staddon, S. (2008) Meta-analysis of the effects of predation on animal prey abundance: evidence from UK vertebrates. *PLoS ONE*, **3**, e2400.
- Hone, J. (1990) Predator-prey theory and feral pig control, with emphasis on evaluation of shooting from a helicopter. *Wildlife Research*, **17**, 123–130.
- Hone, J. (1994) *Analysis of Vertebrate Pest Control*. Cambridge University Press, Cambridge, UK.
- Hosack, G.R., Peters, G.W. & Hayes, K.R. (2012) Estimating density dependence and latent population trajectories with unknown observation error. *Methods in Ecology and Evolution*, **3**, 1028–1038.
- Hudson, L.N., Isaac, N.J.B. & Reuman, D.C. (2013) The relationship between body mass and field metabolic rate among individual birds and mammals. *Journal of Animal Ecology*, **82**, 1009–1020.
- Hulbert, A.J., Pamplona, R., Buffenstein, R. & Buttemer, W.A. (2007) Life and death: metabolic rate, membrane composition, and life span of animals. *Physiological Reviews*, **87**, 1175–1213.
- Huxley, J.S. (1932) *Problems of Relative Growth*. Methuen, London, UK.
- Iijima, H., Nagaike, T. & Honda, T. (2013) Estimation of deer population dynamics using a bayesian state-space model with multiple abundance indices. *The Journal of Wildlife Management*, **77**, 1038–1047.
- IWGS. (2005) *Report of the Independent Working Group on Snares*. Defra, London, UK.
- Jackson, D.A. & Somers, K.M. (1991) The spectre of ‘spurious’ correlations. *Oecologia*, **86**, 147–151.
- Jacquot, M., Coeurdassier, M., Couval, G., Renaude, R., Pleydell, D., Truchetet, D., Raoul, F. & Giraudoux, P. (2013) Using long-term monitoring of red fox populations to assess changes in rodent control practices (ed P Stephens). *Journal of Applied Ecology*, **50**, 1406–1414.
- Johnson, F.A., Moore, C.T., Kendall, W.L., Dubovsky, J.A., Caithamer, D.F., Kelley, J.R. & Williams, B.K. (1997) Uncertainty and the management of mallard harvests. *Journal of Wildlife Management*, **61**, 202–216.
- Johnson, D.H., Sargeant, A.B. & Allen, S.H. (1975) Fitting Richards’ Curve to data of diverse origins. *Growth*, **39**, 315.
- Jones, O.R., Gaillard, J.-M., Tuljapurkar, S., Alho, J.S., Armitage, K.B., Becker, P.H., Bize, P., Brommer, J., Charmantier, A., Charpentier, M., Clutton-Brock, T., Dobson, F.S., Festa-Bianchet, M., Gustafsson, L., Jensen, H., Jones, C.G., Lillandt, B.-G., McCleery, R., Merilä,

- J., Neuhaus, P., Nicoll, M.A.C., Norris, K., Oli, M.K., Pemberton, J., Pietiäinen, H., Ringsby, T.H., Roulin, A., Saether, B.-E., Setchell, J.M., Sheldon, B.C., Thompson, P.M., Weimerskirch, H., Jean Wickings, E. & Coulson, T. (2008) Senescence rates are determined by ranking on the fast–slow life-history continuum. *Ecology Letters*, **11**, 664–673.
- Jongman, R.H.G. & Bunce, R.G.H. (2009) *Farmland Features in the European Union: A Description and Pilot Inventory of Their Distribution*. Alterra, Wageningen.
- Kaplan, E.L. & Meier, P. (1958) Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association*, **53**, 457–481.
- Kay, B., Gifford, E., Perry, R. & van de Ven, R. (2000) Trapping efficiency for foxes (*Vulpes vulpes*) in central New South Wales: age and sex biases and the effects of reduced fox abundance. *Wildlife Research*, **27**, 547–552.
- Keith, D.A., Martin, T.G., McDonald-Madden, E. & Walters, C. (2011) Uncertainty and adaptive management for biodiversity conservation. *Biological Conservation*, **144**, 1175–1178.
- Kell, L.T., De Oliveira, J.A.A., Punt, A.E., McAllister, M.K. & Kuikka, S. (2006) Operational management procedures: an introduction to the use of management strategy evaluation frameworks. In *The Knowledge Base for Fisheries Management Developments in Aquaculture and Fisheries Science*. (eds L. Motos & Wilson), pp. 379–407. Elsevier, Amsterdam, Netherlands.
- Kenchington, T.J. (2014) Natural mortality estimators for information-limited fisheries. *Fish and Fisheries*, **15**, 533–562.
- Kendall, B.E. (1998) Estimating the magnitude of environmental stochasticity in survivorship data. *Ecological Applications*, **8**, 184–193.
- Kenney, B.C. (1982) Beware of spurious self-correlations! *Water Resources Research*, **18**, 1041–1048.
- Kéry, M. (2010) *Introduction to WinBUGS for Ecologists Bayesian Approach to Regression, ANOVA, Mixed Models and Related Analyses*. Elsevier, Amsterdam, Netherlands.
- Kéry, M. & Schaub, M. (2012) State-Space Models for Population Counts. *Bayesian Population Analysis using WinBUGS* (eds M. Kéry & M. Schaub), pp. 115–132. Academic Press, Boston, MA, USA.
- King, R., Morgan, B.J.T., Gimenez, O. & Brooks, S.P. (2010) *Bayesian Analysis for Population Ecology*. Chapman & Hall/CRC, Boca Raton, FL, USA.
- Kinnear, J.E., Onus, M.L. & Bromilow, R.N. (1988) Fox control and rock-wallaby population dynamics. *Wildlife Research*, **15**, 435–450.

- Kirkwood, G.P. (1997) The revised management procedure of the International Whaling Commission. *Global trends: fishery management* (eds E.K. Pikitch, D.D. Huppert & M.P. Sissenwine), pp. 91–99. Bethesda, MD, USA.
- Kleiber, M. (1932) Body size and metabolism. *Hilgardia*, **6**, 315–332.
- Knape, J. (2008) Estimability of density dependence in models of time series data. *Ecology*, **89**, 2994–3000.
- Knape, J., Besbeas, P. & de Valpine, P. (2013) Using uncertainty estimates in analyses of population time series. *Ecology*, **94**, 2097–2107.
- Knape, J., Jonzén, N. & Sköld, M. (2011) On observation distributions for state space models of population survey data. *Journal of Animal Ecology*, **80**, 1269–1277.
- Knaus, J. (2013) *Snowfall: Easier Cluster Computing (based on Snow)*.
- Kolb, H.H. & Hewson, R. (1980) A study of fox populations in Scotland from 1971 to 1976. *Journal of Applied Ecology*, **17**, 7–19.
- Krebs, C.J., Boutin, S., Boonstra, R., Sinclair, A.R.E., Smith, J.N.M., Dale, M.R.T., Martin, K. & Turkington, R. (1995) Impact of food and predation on the snowshoe hare cycle. *Science*, **269**, 1112–1115.
- Kuhnert, P.M., Martin, T.G. & Griffiths, S.P. (2010) A guide to eliciting and using expert knowledge in Bayesian ecological models. *Ecology Letters*, **13**, 900–914.
- Van Langevelde, F., van Dooremalen, C. & Jaarsma, C.F. (2009) Traffic mortality and the role of minor roads. *Journal of Environmental Management*, **90**, 660–667.
- Van Langevelde, F. & Jaarsma, C. (2004) Using traffic flow theory to model traffic mortality in mammals. *Landscape Ecology*, **19**, 895–907.
- Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.
- Lebreton, J.-D. & Gimenez, O. (2013) Detecting and estimating density dependence in wildlife populations. *The Journal of Wildlife Management*, **77**, 12–23.
- Leopold, A. (1933) *Game Management*. University of Wisconsin Press, Madison, WI, USA.
- Leslie, P.H. & Davis, D.H.S. (1939) An attempt to determine the absolute number of rats on a given area. *Journal of Animal Ecology*, **8**, 94–113.
- Levine, R.V. & Norenzayan, A. (1999) The Pace of Life in 31 Countries. *Journal of Cross-Cultural Psychology*, **30**, 178–205.

- Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T. & Sand, H. (2012) Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society of London: Biological Sciences*.
- Lindström, E.R. (1981) Reliability of placental scar counts in the red fox (*Vulpes vulpes* L.) with special reference to fading of the scars. *Mammal Review*, **11**, 137–149.
- Lindström, E.R. (1988) Reproductive effort in the red fox, *Vulpes vulpes*, and future supply of a fluctuating prey. *Oikos*, **52**, 115–119.
- Lindström, E.R. (1992) Diet and demographics of the red fox (*Vulpes vulpes*) in relation to population density - the sarcoptic mange event in Scandinavia. *Wildlife 2001: Populations* (eds D.R. McCullough & R.H. Barrett), pp. 922–931. Elsevier Applied Science, London, UK.
- Lindström, E.R. (1994) Large prey for small cubs: on crucial resources of a boreal red fox population. *Ecography*, **17**, 17–22.
- Linhart, S.B. (1968) Dentition and pelage in the juvenile red fox (*Vulpes vulpes*). *Journal of Mammalogy*, **49**, 526–528.
- Lloyd, H.G. (1980) *The Red Fox*. Batsford, London, UK.
- Lloyd, H.G. & Englund, J. (1973) The reproductive cycle of the red fox in Europe. *Journal of Reproduction and Fertility Supplement*, **19**, 119–130.
- Long, R.A., MacKay, P., Zielinski, W.J. & Ray, J.C. (eds). (2008) *Noninvasive Survey Methods for Carnivores*. Island Press, Washington, DC, USA.
- Lorenzen, K. (1996) The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *Journal of Fish Biology*, **49**, 627–647.
- Macdonald, D.W. (1979) ‘Helpers’ in fox society. *Nature*, **282**, 69–71.
- Macdonald, D.W. (1980a) Patterns of scent marking with urine and faeces amongst carnivore communities. pp. 107–139.
- Macdonald, D.W. (1980b) Social factors affecting reproduction amongst red foxes (*Vulpes vulpes* L., 1758). *The Red Fox: Symposium on Behaviour and Ecology* (ed E. Zimen), pp. 123–175. Dr. W. Junk bv Publishers, The Hague, Netherlands.
- Macdonald, D.W. (1981) Resource dispersion and the social organisation of the red fox (*Vulpes vulpes*). *Proceedings of the Worldwide Furbearer Conference* (eds J.A. Chapman & D. Pursley), pp. 918–949. University of Maryland Press, Maryland.
- Macdonald, D.W. (1983) The ecology of carnivore social behaviour. *Nature*, **301**, 379–384.

- Macdonald, D.W., Bunce, R.G.H. & Bacon, P.J. (1981) Fox populations, habitat characterization and rabies control. *Journal of Biogeography*, **8**, 145–151.
- Macdonald, D.W. & Reynolds, J.C. (2004) Red Fox *Vulpes vulpes*. *Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan* (eds C. Sillero-Zubiri, M. Hoffmann & D.W. Macdonald), pp. 129–136. IUCN/SSC Canid Specialist Group, Gland, Switzerland and Cambridge, UK.
- Macdonald, D.W., Reynolds, J.C., Carbone, C., Mathews, F. & Johnson, P.J. (2003) The bio-economics of fox control. *Conservation & Conflict: Mammals & Farming in Britain* Linnaean Society Occasional Publication. (eds F. Tattersall & W. Manley), pp. 220–236. Westbury Publishing, Otley, Yorkshire, UK.
- Macdonald, D.W. & Voigt, D.R. (1985) The biological basis of rabies models. *Population Dynamics of Rabies in Wildlife* (ed P.J. Bacon), pp. 71–108. Academic Press, London, UK.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2006) *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Elsevier, San Diego, CA, USA.
- MacNulty, D.R., Smith, D.W., Vucetich, J.A., Mech, L.D., Stahler, D.R. & Packer, C. (2009) Predatory senescence in ageing wolves. *Ecology Letters*, **12**, 1347–1356.
- Maekawa, K., Yoneda, M. & Togashi, H. (1980) A preliminary study of the age structure of the red fox in Eastern Hokkaido. *Japanese Journal of Ecology*, **30**, 103–108.
- Magnusson, A. & Hilborn, R. (2007) What makes fisheries data informative? *Fish and Fisheries*, **8**, 337–358.
- Marcström, V. (1968) Tagging studies on red fox (*Vulpes v.*) in Sweden. *Viltrevy*, **5**, 103–117.
- Martin, T.G., Arcese, P., Kuhnert, P.M., Gaston, A.J. & Martin, J.-L. (2013) Prior information reduces uncertainty about the consequences of deer overabundance on forest birds. *Biological Conservation*, **165**, 10–17.
- Martin, T.G., Kuhnert, P.M., Mengersen, K. & Possingham, H.P. (2005) The power of expert opinion in ecological models using Bayesian methods: impact of grazing on birds. *Ecological Applications*, **15**, 266–280.
- Martin, J., O'Connell, A.F., Kendall, W.L., Runge, M.C., Simons, T.R., Waldstein, A.H., Schulte, S.A., Converse, S.J., Smith, G.W., Pinion, T., Rikard, M. & Zipkin, E.F. (2010) Optimal control of native predators. *Biological Conservation*, **143**, 1751–1758.
- Maurel, D., Lacroix, A. & Boissin, J. (1984) Seasonal reproductive endocrine profiles in two wild mammals: the red fox (*Vulpes vulpes* L.) and the European badger (*Meles meles* L.) considered as short-day mammals. *Acta endocrinologica*, **105**, 130–138.

- McAllister, M.K. (2014) A generalized Bayesian surplus production stock assessment software (BSP2). *ICCAT (International Commission for the Conservation of Atlantic Tunas) Collective Volume of Scientific Papers*, **70**, 1725–1757.
- McAllister, M.K., Hill, S.L., Agnew, D.J., Kirkwood, G.P. & Beddington, J.R. (2004) A Bayesian hierarchical formulation of the De Lury stock assessment model for abundance estimation of Falkland Islands' squid (*Loligo gahi*). *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 1048–1059.
- McAllister, M.K. & Kirkwood, G.P. (1998) Bayesian stock assessment: a review and example application using the logistic model. *ICES Journal of Marine Science*, **55**, 1031–1060.
- McAllister, M.K., Pikitch, E.K. & Babcock, E.A. (2001) Using demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 1871–1890.
- McAllister, M.K., Pikitch, E.K., Punt, A.E. & Hilborn, R. (1994) A Bayesian approach to stock assessment and harvest decisions using the sampling/importance resampling algorithm. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 2673–2687.
- McAllister, M.K., Stanley, R.D. & Starr, P. (2010) Using experiments and expert judgement to model catchability of Pacific rockfishes in trawl surveys, with application to bocaccio (*Sebastes paucispinis*) off British Columbia. *Fishery Bulletin*, **108**, 282–304.
- McAllister, M.K., Starr, P.J., Restrepo, V.R. & Kirkwood, G.P. (1999) Formulating quantitative methods to evaluate fishery-management systems: what fishery processes should be modelled and what trade-offs should be made? *ICES Journal of Marine Science*, **56**, 900–916.
- McCarthy, M.A. (2007) *Bayesian Methods for Ecology*. Cambridge University Press, Cambridge, UK.
- McCarthy, M.A., Citroen, R. & McCall, S.C. (2008) Allometric scaling and Bayesian priors for annual survival of birds and mammals. *The American Naturalist*, **172**, 216–222.
- McCarthy, M.A. & Masters, P. (2005) Profiting from prior information in Bayesian analyses of ecological data. *Journal of Applied Ecology*, **42**, 1012–1019.
- McCoy, M.W. & Gillooly, J.F. (2008) Predicting natural mortality rates of plants and animals. *Ecology Letters*, **11**, 710–716.
- McDonald, R.A. & Harris, S. (1999) The use of trapping records to monitor populations of stoats *Mustela erminea* and weasels *M. nivalis*: the importance of trapping effort. *Journal of Applied Ecology*, **36**, 679–688.

- McIlroy, J., Saunders, G. & Hinds, L.A. (2001) The reproductive performance of female red foxes, *Vulpes vulpes*, in central-western New South Wales during and after a drought. *Canadian Journal of Zoology*, **79**, 545–553.
- McLeod, S.R. & Saunders, G. (2014) Fertility control is much less effective than lethal baiting for controlling foxes. *Ecological Modelling*, **273**, 1–10.
- Met Office. (2011) Regional climate values for the Mean Temperature, <http://data.gov.uk/dataset/regional-climate-values-for-mean-temperature>
- Meyer, R. & Millar, R.B. (1999a) BUGS in Bayesian stock assessments. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1078–1086.
- Meyer, R. & Millar, R.B. (1999b) Bayesian stock assessment using a state–space implementation of the delay difference model. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 37–52.
- Millar, R.B. & Meyer, R. (2000a) Bayesian state–space modeling of age-structured data: fitting a model is just the beginning. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 43–50.
- Millar, R.B. & Meyer, R. (2000b) Non-linear state space modelling of fisheries biomass dynamics by using Metropolis-Hastings within-Gibbs sampling. *Applied Statistics*, **49**, 327–342.
- Milner-Gulland, E.J. (2011) Integrating fisheries approaches and household utility models for improved resource management. *Proceedings of the National Academy of Sciences*, **108**, 1741–1746.
- Milner-Gulland, E.J., Arroyo, B., Bellard, C., Blanchard, J., Bunnefeld, N., Delibes-Mateos, M., Edwards, C., Nuno, A., Palazy, L., Reljic, S., Riera, P. & Skrbinek, T. (2010) New directions in management strategy evaluation through cross-fertilization between fisheries science and terrestrial conservation. *Biology Letters*, **6**, 719–722.
- Moberly, R.L., White, P.C.L., Webbon, C.C., Baker, P.J. & Harris, S. (2003) Factors associated with fox (*Vulpes vulpes*) predation of lambs in Britain. *Wildlife Research*, **30**, 219–227.
- Mohler, B., Thompson, W., Creem-Regehr, S., Pick, H., Jr & Warren, W., Jr. (2007) Visual flow influences gait transition speed and preferred walking speed. *Experimental Brain Research*, **181**, 221–228.
- Mulder, J.L. (2004) Longevity records in the red fox. *Lutra*, **47**, 51–52.
- Newman, K.B., Fernández, C., Thomas, L. & Buckland, S.T. (2009) Monte Carlo inference for state–space models of wild animal populations. *Biometrics*, **65**, 572–583.

- Nichols, J.D. & Pollock, K.H. (1990) Estimation of recruitment from immigration versus in situ reproduction using Pollock's robust design. *Ecology*, **71**, 21–26.
- Nussey, D.H., Coulson, T., Festa-Bianchet, M. & Gaillard, J.M. (2008) Measuring senescence in wild animal populations: towards a longitudinal approach. *Functional Ecology*, **22**, 393–406.
- O'Hara, R.B., Lampila, S. & Orell, M. (2009) Estimation of rates of births, deaths, and immigration from mark–recapture data. *Biometrics*, **65**, 275–281.
- Ohsumi, S. (1979) Interspecies relationships among some biological parameters in cetaceans and estimation of the natural mortality coefficient of the southern hemisphere minke whale. *Report of the International Whaling Commission*, **29**, 397–406.
- Ono, K., Punt, A.E. & Rivot, E. (2012) Model performance analysis for Bayesian biomass dynamics models using bias, precision and reliability metrics. *Fisheries Research*, **125–126**, 173–183.
- Österholm, H. (1964) The significance of distance receptors in the feeding behaviour of the fox (*Vulpes vulpes*). *Acta Zoologica Fennica*, **106**, 1–31.
- Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978) Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, **62**, 3–135.
- PACEC. (2006) *The Economic and Environmental Impact of Sport Shooting*. Public and Corporate Economic Consultants, Cambridge, UK.
- Page, R.J.C. (1981) Dispersal and population density of the fox (*Vulpes vulpes*) in an area of London. *Journal of Zoology*, **194**, 485–491.
- Paloheimo, J.E. & Dickie, L.M. (1964) Abundance and fishing success. *Rapports et procès-verbaux réunions, Conseil International pour l'Exploration de la Mer*, **155**, 152–163.
- Parkes, J.P., Robley, A., Forsyth, D.M. & Choquenot, D. (2006) Adaptive management experiments in vertebrate pest control in New Zealand and Australia. *Wildlife Society Bulletin*, **34**, 229–236.
- Parma, A., Amarasekare, P., Mangel, M., Moore, J., Murdoch, W.W., Noonburg, E., Pascual, M.A., Possingham, H.P., Shea, K., Wilcox, C. & Yu, D. (1998) What can adaptive management do for our fish, forests, food and biodiversity? *Integrative Biology*, **1**, 16–26.
- Parma, A.M. & Deriso, R.B. (1990) Experimental harvesting of cyclic stocks in the face of alternative recruitment hypotheses. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 595–610.
- Pauly, D. (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour*

l'Exploration de la Mer, **39**, 175–192.

Pearson, K. (1897) Mathematical Contributions to the Theory of Evolution.--On a Form of Spurious Correlation Which May Arise When Indices Are Used in the Measurement of Organs. *Proceedings of the Royal Society of London*, **60**, 489–498.

Peery, M.Z., Becker, B.H. & Beissinger, S.R. (2006) Combining demographic and count-based approaches to identify source-sink dynamics of a threatened seabird. *Ecological Applications*, **16**, 1516–1528.

Pence, D.B. & Windberg, L.A. (1994) Impact of a sarcoptic mange epizootic on a coyote population. *The Journal of Wildlife Management*, **58**, 624–633.

Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, UK.

Pils, C.M. & Martin, M.A. (1978) *Population Dynamics, Predator-Prey Relationships and Management of the Red Fox in Wisconsin*. Technical Bulletin, Department of Natural Resources, Madison, WI.

Plummer, M., Best, N., Cowles, K. & Vines, K. (2006) CODA: Convergence Diagnosis and Output Analysis for MCMC. *R News*, **6**, 7–11.

Pollock, K.H., Conroy, M.J. & Hearn, W.S. (1995) Separation of hunting and natural mortality using ring-return models: an overview. *Journal of Applied Statistics*, **22**, 557–566.

Pollock, K.H., Winterstein, S.R., Bunck, C.M. & Curtis, P.D. (1989) Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management*, **53**, 7–15.

Pope, J.G. & Knights, B.J. (1982) Simple models of predation in multi-age multispecies fisheries for considering the estimation of fishing mortality and its effects. *Multispecies approaches to fisheries management advice* Canadian Special Publication of Fisheries and Aquatic Sciences. (ed M.C. Mercer), pp. 64–69.

Porteus, T.A., Richardson, S.M. & Reynolds, J.C. (2011) The importance of survey design in distance sampling: field evaluation using domestic sheep. *Wildlife Research*, **38**, 221–234.

Porteus, T.A., Short, M.J., Richardson, S.M. & Reynolds, J.C. (2012) Empirical development of strategy for the control of invasive American mink by trapping. *European Journal of Wildlife Research*, **58**, 403–413.

Potts, G.R. (1980) The effects of modern agriculture, nest predation and game management on the population ecology of partridges (*Perdix perdix* and *Alectoris rufa*). *Advances in Ecological Research* (ed A. MacFadyen), pp. 1–79. Academic Press.

Potts, G.R. (2012) *Partridges: Countryside Barometer*. Harper-Collins, London, UK.

- Prato, T. (2005) Bayesian adaptive management of ecosystems. *Ecological Modelling*, **183**, 147–156.
- Promislow, D.E.L. (1991) Senescence in natural populations of mammals: a comparative study. *Evolution*, **45**, 1869–1887.
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *The American Naturalist*, **132**, 652–661.
- Punt, A.E. & Hilborn, R. (1997) Fisheries stock assessment and decision analysis: the Bayesian approach. *Reviews in Fish Biology and Fisheries*, **7**, 35–63.
- Rademeyer, R.A., Plagányi, É.E. & Butterworth, D.S. (2007) Tips and tricks in designing management procedures. *ICES Journal of Marine Science: Journal du Conseil*, **64**, 618–625.
- Ralston, S. (1987) Mortality rates of snappers and groupers. *Tropical Snappers and Groupers: biology and fisheries management* (eds J.J. Polovina & S. Ralston), pp. 375–404. Westview Press, Boulder, CO, USA.
- R Core Team. (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reckhow, K.H. (1990) Bayesian inference in non-replicated ecological studies. *Ecology*, **71**, 2053–2059.
- Reynolds, J.C. (1994) Winter lamping for foxes. *Game Conservancy Trust Review*, **26**, 111–114.
- Reynolds, J.C. (2000) *Fox Control in the Countryside*. The Game Conservancy Trust, Fordingbridge, UK.
- Reynolds, J.C. (2004) Trade-offs between welfare, conservation, utility and economics in wildlife management - a review of conflicts, compromises and regulation. *Animal Welfare*, **13**, 133–138.
- Reynolds, J.C. & Aebischer, N.J. (1991) Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. *Mammal Review*, **21**, 97–122.
- Reynolds, J.C., Goddard, H.N. & Brockless, M.H. (1993) The impact of local fox (*Vulpes vulpes*) removal on fox populations at two sites in southern England. *Gibier Faune Sauvage*, **10**, 319–334.
- Reynolds, J.C., Porteus, T.A., Richardson, S.M., Leigh, R.J. & Short, M.J. (2010a) Detectability of American mink using rafts to solicit field signs in a population control context. *Journal of Wildlife Management*, **74**, 1601–1606.

- Reynolds, J.C., Richardson, S.M., Rodgers, B.J.E. & Rodgers, O.R.K. (2013) Effective control of non-native American mink by strategic trapping in a river catchment in mainland Britain. *The Journal of Wildlife Management*, **77**, 545–554.
- Reynolds, J.C., Stoate, C., Brockless, M.H., Aebischer, N.J. & Tapper, S.C. (2010b) The consequences of predator control for brown hares (*Lepus europaeus*) on UK farmland. *European Journal of Wildlife Research*, **56**, 541–549.
- Reynolds, J.C. & Tapper, S.C. (1993) Are foxes on the increase? *Game Conservancy Trust Review*, **25**, 94–96.
- Reynolds, J.C. & Tapper, S.C. (1995a) The ecology of the red fox *Vulpes vulpes* in relation to small game in rural southern England. *Wildlife Biology*, **1**, 105–119.
- Reynolds, J.C. & Tapper, S.C. (1995b) Predation by foxes *Vulpes vulpes* on brown hares *Lepus europaeus* in central southern England, and its potential impact on annual population growth. *Wildlife Biology*, **1**, 145–158.
- Reynolds, J.C. & Tapper, S.C. (1996) Control of mammalian predators in game management and conservation. *Mammal Review*, **26**, 127–156.
- Ricker, W.E. (1975) Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada*, **191**, 382 p.
- Ricklefs, R.E. (1998) Evolutionary theories of aging: confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. *The American Naturalist*, **152**, 24–44.
- Ricklefs, R.E. (2008) The evolution of senescence from a comparative perspective. *Functional Ecology*, **22**, 379–392.
- Ricklefs, R.E. (2010a) Insights from comparative analyses of aging in birds and mammals. *Aging Cell*, **9**, 273–284.
- Ricklefs, R.E. (2010b) Life-history connections to rates of aging in terrestrial vertebrates. *Proceedings of the National Academy of Sciences*, **107**, 10314–10319.
- Ricklefs, R.E. & Scheuerlein, A. (2001) Comparison of aging-related mortality among birds and mammals. *Experimental Gerontology*, **36**, 845–857.
- Ricklefs, R.E. & Scheuerlein, A. (2002) Biological implications of the Weibull and Gompertz models of aging. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, **57**, B69–B76.
- Rist, J., Rowcliffe, M., Cowlishaw, G. & Milner-Gulland, E.J. (2008) Evaluating measures of hunting effort in a bushmeat system. *Biological Conservation*, **141**, 2086–2099.

- Rivera-Milán, F.F., Boomer, G.S. & Martínez, A.J. (2014) Monitoring and modeling of population dynamics for the harvest management of scaly-naped pigeons in Puerto Rico. *The Journal of Wildlife Management*, **78**, 513–521.
- Robert, M., Faraj, A., McAllister, M.K. & Rivot, E. (2010) Bayesian state-space modelling of the De Lury depletion model: strengths and limitations of the method, and application to the Moroccan octopus fishery. *ICES Journal of Marine Science: Journal du Conseil*, **67**, 1272–1290.
- Robertson, P.A. (1991) Estimating the nesting success and productivity of British pheasants *Phasianus colchicus* from nest-record schemes. *Bird Study*, **38**, 73–79.
- Robertson, P.A. & Dowell, S.D. (1990) The effects of hand rearing on wild gamebird populations. *The Future of wild Galliformes in the Netherlands: Symposium : Papers and discussion*. (eds J.T. Lumeij & Y.R. Hoogeveen), pp. 158–171. Organisatie Commissie Nederlandse Wilde Hoenders, Amersfoort, Netherlands.
- Robertson, P. & Hill, D. (1992) A bird in the bush is worth four in the hand - hand-rearing and the productivity of pheasants in the wild. *Global Trends in Wildlife Management* (eds B. Bobek, K. Perzanowski & W. Regelin), pp. 305–309. Swiat Press, Krakow-Warszawa, Poland.
- Robinson, H.S., Wielgus, R.B., Cooley, H.S. & Cooley, S.W. (2008) Sink populations in carnivore management: cougar demography and immigration in a hunted population. *Ecological Applications*, **18**, 1028–1037.
- Rogers, D. (1972) Random search and insect population models. *Journal of Animal Ecology*, **41**, 369–383.
- Roseberry, J.L. & Woolf, A. (1991) A comparative evaluation of techniques for analysing white-tailed deer harvest data. *Wildlife Monographs*, **117**, 3–59.
- Ruette, S., Stahl, P. & Albaret, M. (2003) Applying distance-sampling methods to spotlight counts of red foxes. *Journal of Applied Ecology*, **40**, 32–43.
- Rushton, S.P., Shirley, M.D.F., Macdonald, D.W. & Reynolds, J.C. (2006) Effects of culling fox populations at the landscape scale: a spatially explicit population modeling approach. *Journal of Wildlife Management*, **70**, 1102–1110.
- Sadler, L.M.J., Webbon, C.C., Baker, P.J. & Harris, S. (2004) Methods of monitoring red foxes *Vulpes vulpes* and badgers *Meles meles*: are field signs the answer? *Mammal Review*, **34**, 75–98.
- Sainsbury, K.J., Punt, A.E. & Smith, A.D.M. (2000) Design of operational management strategies for achieving fishery ecosystem objectives. *ICES Journal of Marine Science: Journal du Conseil*, **57**, 731–741.

- Salo, P., Banks, P.B., Dickman, C.R. & Korpimäki, E. (2010) Predator manipulation experiments: impacts on populations of terrestrial vertebrate prey. *Ecological Monographs*, **80**, 531–546.
- Samuel, M.D., Garton, E.O., Schlegel, M.W. & Carson, R.G. (1987) Visibility bias during aerial surveys of elk in northcentral Idaho. *Journal of Wildlife Management*, **51**, 622–630.
- Sargeant, A.B. (1978) Red fox prey demands and implications to Prairie duck production. *Journal of Wildlife Management*, **42**, 520–527.
- Savage, V.M., Allen, A.P., Brown, J.H., Gillooly, J.F., Herman, A.B., Woodruff, W.H. & West, G.B. (2007) Scaling of number, size, and metabolic rate of cells with body size in mammals. *Proceedings of the National Academy of Sciences*, **104**, 4718–4723.
- Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B. & Charnov, E. (2004a) Effects of body size and temperature on population growth. *The American Naturalist*, **163**, 429–441.
- Savage, V.M., Gillooly, J.F., Woodruff, W.H., West, G.B., Allen, A.P., Enquist, B.J. & Brown, J.H. (2004b) The predominance of quarter power scaling in biology. *Functional Ecology*, **18**, 257–282.
- Schaefer, M.B. (1957) A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. *Bulletin of the Inter-American Tropical Tuna Commission*, **2**, 247–285.
- Schaub, M. & Abadi, F. (2011) Integrated population models: a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology*, **152**, 227–237.
- Schnute, J.T. (1994) A general framework for developing sequential fisheries models. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 1676–1688.
- Seber, G.A.F. (1982) *The Estimation of Animal Abundance and Related Parameters*, Second. Charles Griffin, London, UK.
- Seiler, A., Helldin, J.-O. & Seiler, C. (2004) Road mortality in Swedish mammals: results of a drivers' questionnaire. *Wildlife Biology*, **10**, 225–233.
- Shea, K., Amarasekare, P., Kareiva, P., Mangel, M., Moore, J., Murdoch, W.W., Noonburg, E., Parma, A.N., Pascual, M.A., Possingham, H.P., Wilcox, C. & Yu, D. (1998) Management of populations in conservation, harvesting and control. *Trends in Ecology & Evolution*, **13**, 371–375.
- Short, M.J., Weldon, A.W., Richardson, S.M. & Reynolds, J.C. (2012) Selectivity and injury risk in an improved neck snare for live-capture of foxes. *Wildlife Society Bulletin*, **36**, 208–219.
- Sibly, R.M., Barker, D., Denham, M.C., Hone, J. & Pagel, M. (2005) On the regulation of

populations of mammals, birds, fish and insects. *Science*, **309**, 607–610.

Sibly, R.M., Collett, D., Promislow, D.E.L., Peacock, D.J. & Harvey, P.H. (1997) Mortality rates of mammals. *Journal of Zoology*, **243**, 1–12.

Silva, M. & Downing, J.A. (1995) *CRC Handbook of Mammalian Body Masses*. CRC Press, Boca Raton, FL, USA.

Sinclair, A.R.E., Fryxell, J.M. & Caughley, G. (2006) *Wildlife Ecology, Conservation and Management*, 2nd ed. Blackwell Publishing, Oxford, UK.

Sinclair, A.R.E., Pech, R.P., Dickman, C.R., Hik, D., Mahon, P.S. & Newsome, A.E. (1998) Predicting effects of predation on conservation of endangered prey. *Conservation Biology*, **12**, 564–575.

Slough, B.G. & Mowat, G. (1996) Lynx population dynamics in an untrapped refugium. *Journal of Wildlife Management*, **60**, 946–961.

Smith, D.W. (1985) A continuous time deterministic model of temporal rabies. *Population Dynamics of Rabies in Wildlife* (ed P.J. Bacon), pp. 131–146. Academic Press, London, UK.

Smith, F.A., Lyons, S.K., Ernest, S.K.M., Jones, K.E., Kaufman, D.M., Dayan, T., Marquet, P.A., Brown, J.H. & Haskell, J.P. (2003) Body mass of late quaternary mammals. *Ecology*, **84**, 3403–3403.

Smith, A.D.M., Sainsbury, K.J. & Stevens, R.A. (1999) Implementing effective fisheries-management systems - management strategy evaluation and the Australian partnership approach. *ICES Journal of Marine Science*, **56**, 967–979.

Smith, A.D.M. & Walters, C.J. (1981) Adaptive management of stock-recruitment systems. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 690–703.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd ed. W.H. Freeman and Company, New York, NY, USA.

Sokos, C.K., Birtsas, P.K. & Tsachalidis, E.P. (2008) The aims of galliforms release and choice of techniques. *Wildlife Biology*, **14**, 412–422.

Soulsbury, C., Baker, P., Iossa, G. & Harris, S. (2008) Fitness costs of dispersal in red foxes (*Vulpes vulpes*). *Behavioral Ecology and Sociobiology*, **62**, 1289–1298.

Soulsbury, C.D., Iossa, G., Baker, P.J., Cole, N.C., Funk, S.M. & Harris, S. (2007) The impact of sarcoptic mange *Sarcoptes scabiei* on the British fox *Vulpes vulpes* population. *Mammal Review*, **37**, 278–296.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & van der Linde, A. (2002) Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society, Series B*, **64**, 583–639.

- Spiegelhalter, D.J., Thomas, A., Best, N.G. & Lunn, D.J. (2007) *WinBUGS*. Medical Research Council Biostatistics Unit, Cambridge, UK.
- Stahl, P. (1990) Influence of age-related changes in prey consumption on correction factors established for important prey of the red fox (*Vulpes vulpes*). *Gibier Faune Sauvage*, **7**, 107–125.
- Stoate, C., Brockless, M.H. & Boatman, N.D. (2002) A multifunctional approach to bird conservation on farmland: a ten-year appraisal. *Aspects of Applied Biology*, **67**, 191–196.
- Stoate, C. & Leake, A.R. (2002) *Where the Birds Sing. The Allerton Project: 10 Years of Conservation on Farmland*. The Game Conservancy Trust with Allerton Research & Educational Trust, Fordingbridge, UK.
- Storm, G.L., Andrews, R.D., Phillips, R.L., Bishop, R.A., Siniff, D.B. & Tester, J.R. (1976) Morphology, reproduction, dispersal, and mortality of Midwestern red fox populations. *Wildlife Monographs*, **49**, 3–82.
- Sturtz, S., Ligges, U. & Gelman, A. (2005) R2WinBUGS: a package for running WinBUGS from R. *Journal of Statistical Software*, **12**, 1–16.
- Su, Z., Peterman, R.M. & Haeseker, S.L. (2004) Spatial hierarchical Bayesian models for stock–recruitment analysis of pink salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 2471–2486.
- Tapper, S.C. (1992) *Game Heritage: An Ecological Review from Shooting and Gamekeeping Records*. The Game Conservancy, Fordingbridge, UK.
- Tapper, S.C. (1999) *A Question of Balance*. The Game Conservancy Trust, Fordingbridge, UK.
- Tapper, S.C., Potts, G.R. & Brockless, M.H. (1996) The effect of an experimental reduction in predation pressure on the breeding success and population density of grey partridges *Perdix perdix*. *Journal of Applied Ecology*, **33**, 965–978.
- Then, A.Y., Hoenig, J.M., Hall, N.G. & Hewitt, D.A. (2014) Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. *ICES Journal of Marine Science: Journal du Conseil*.
- Therneau, T. (2014) *A Package for Survival Analysis in S*.
- Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R., Marques, T.A. & Burnham, K.P. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, **47**, 5–14.
- Thomson, P.C., Marlow, N.J., Rose, K. & Kok, N.E. (2000) The effectiveness of a large-

scale baiting campaign and an evaluation of a buffer zone strategy for fox control. *Wildlife Research*, **27**, 465–472.

Thorarinsdóttir, G.G., Jacobson, L., Ragnarsson, S.Á., Garcia, E.G. & Gunnarsson, K. (2010) Capture efficiency and size selectivity of hydraulic clam dredges used in fishing for ocean quahogs (*Arctica islandica*): simultaneous estimation in the SELECT model. *ICES Journal of Marine Science*, **67**, 345–354.

Thorson, J.T., Ono, K. & Munch, S.B. (2014) A Bayesian approach to identifying and compensating for model misspecification in population models. *Ecology*, **95**, 329–341.

Tobler, W. (1993) *Non-Isotropic Geographic Modeling*. Technical Report, National Center for Geographic Information and Analysis, University of California, Santa Barbara, CA.

Toïgo, C., Servanty, S., Gaillard, J.-M., Brandt, S. & Baubet, E. (2008) Disentangling natural from hunting mortality in an intensively hunted wild boar population. *Journal of Wildlife Management*, **72**, 1532–1539.

Tome, M.W. (1988) Optimal foraging: food patch depletion by ruddy ducks. *Oecologia*, **76**, 27–36.

Trenkel, V.M. (2001) Exploring red deer culling strategies using a population-specific calibrated management model. *Journal of Environmental Management*, **62**, 37–53.

Trenkel, V.M. (2008) A two-stage biomass random effects model for stock assessment without catches: What can be estimated using only biomass survey indices? *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 1024–1035.

Trewby, I.D., Wilson, G.J., Delahay, R.J., Walker, N., Young, R.P., Davison, J., Cheeseman, C.L., Robertson, P.A., Gorman, M.L. & McDonald, R.A. (2008) Experimental evidence of competitive release in sympatric carnivores. *Biology Letters*, **4**, 170–172.

Trewhella, W.J. & Harris, S. (1988) A simulation model of the pattern of dispersal in urban fox (*Vulpes vulpes*) populations and its application for rabies control. *Journal of Applied Ecology*, **25**, 435–450.

Trewhella, W.J., Harris, S. & McAllister, F.E. (1988) Dispersal distance, home range size and population density in the red fox (*Vulpes vulpes*): a quantitative analysis. *Journal of Applied Ecology*, **25**.

Trombulak, S.C. & Frissell, C.A. (2000) Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, **14**, 18–30.

Trout, R.C., Langton, S., Smith, G.C. & Haines-Young, R.H. (2000) Factors affecting the abundance of rabbits (*Oryctolagus cuniculus*) in England and Wales. *Journal of Zoology*, **252**, 227–238.

- Uraguchi, K., Ueno, M., Iijima, H. & Saitoh, T. (2014) Demographic analyses of a fox population suffering from sarcoptic mange. *The Journal of Wildlife Management*, **78**, 1356–1371.
- De Valpine, P. & Hastings, A. (2002) Fitting population models incorporating process noise and observation error. *Ecological Monographs*, **72**, 57–76.
- Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, 4th ed. Springer, New York, NY, USA.
- Venturato, E., Cavallini, P. & Dessì-Fulgheri, F. (2010) Are pheasants attracted or repelled by roads? A test of a crucial assumption for transect censuses. *European Journal of Wildlife Research*, **56**, 233–237.
- Vetter, E.F. (1988) Estimation of natural mortality in fish stocks: a review. *Fishery Bulletin*, **86**, 25–43.
- Voigt, D.R. & Macdonald, D.W. (1984) Variation in the spatial and social behaviour of the red fox, *Vulpes vulpes*. *Acta Zoologica Fennica*, **171**, 261–265.
- Wade, P.R. (2000) Bayesian methods in conservation biology. *Conservation Biology*, **14**, 1308–1316.
- Walsh, A.L. & Harris, S. (1996) Factors determining the abundance of vespertilionid bats in Britain: geographical, land class and local habitat relationships. *Journal of Applied Ecology*, **33**, 519–529.
- Walters, C.J. (1986) *Adaptive Management of Renewable Resources*. Blackburn Press, Caldwell, NJ, USA.
- Walters, C. (2004) Simple representation of the dynamics of biomass error propagation for stock assessment models. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 1061–1065.
- Walters, C.J. (2007) Is adaptive management helping to solve fisheries problems? *Ambio*, **36**, 304–307.
- Walters, C.J. & Hilborn, R. (1976) Adaptive control of fishing systems. *Journal of the Fisheries Research Board of Canada*, **33**, 145–159.
- Walters, C.J. & Ludwig, D. (1994) Calculation of Bayes posterior probability distributions for key population parameters. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 713–722.
- Walters, C.J. & Martell, S.J.D. (2004) *Fisheries Ecology and Management*. Princeton University Press, Princeton, NJ, USA.

- Wandeler, P., Funk, S.M., Largiadèr, C.R., Gloor, S. & Breitenmoser, U. (2003) The city-fox phenomenon: genetic consequences of a recent colonization of urban habitat. *Molecular Ecology*, **12**, 647–656.
- Webbon, C.C., Baker, P.J., Cole, N.C. & Harris, S. (2006) Macroscopic prey remains in the winter diet of foxes *Vulpes vulpes* in rural Britain. *Mammal Review*, **36**, 85–97.
- Webbon, C.C., Baker, P.J. & Harris, S. (2004) Faecal density counts for monitoring changes in red fox numbers in rural Britain. *Journal of Applied Ecology*, **41**, 768–779.
- Wenger, S.J. & Freeman, M.C. (2008) Estimating species occurrence, abundance, and detection probability using zero-inflated distributions. *Ecology*, **89**, 2953–2959.
- West, G.B. & Brown, J.H. (2005) The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization. *Journal of Experimental Biology*, **208**, 1575–1592.
- West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science*, **276**, 122–126.
- White, G.C. (2005) Correcting wildlife counts using detection probabilities. *Wildlife Research*, **32**, 211–216.
- White, G.C., Anderson, D.R., Burnham, K.P. & Otis, D.L. (1982) *Capture–recapture and Removal Methods for Sampling Closed Populations*. Los Alamos National Laboratory, Los Alamos, NM.
- White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, 120–139.
- White, P.C.L., Saunders, G. & Harris, S. (1996) Spatio-temporal patterns of home range use by foxes (*Vulpes vulpes*) in urban environments. *Journal of Animal Ecology*, **65**, 121–125.
- White, C.R. & Seymour, R.S. (2005) Allometric scaling of mammalian metabolism. *Journal of Experimental Biology*, **208**, 1611–1619.
- White, P.J.C., Stoate, C., Szczer, J. & Norris, K. (2014) Predator reduction with habitat management can improve songbird nest success. *The Journal of Wildlife Management*, **78**, 402–412.
- Whitlock, R.E., Aebischer, N.J. & Reynolds, J.C. (2003) *The National Gamebag Census as a Tool for Monitoring Mammal Abundance in the UK*. The Game Conservancy Trust, Fordingbridge, UK.
- Whitlock, R.E., McAllister, M.K. & Block, B.A. (2012) Estimating fishing and natural mortality rates for Pacific bluefin tuna (*Thunnus orientalis*) using electronic tagging data. *Fisheries Research*, **119–120**, 115–127.

- Williams, B.K. (1996) Adaptive optimization and the harvest of biological populations. *Mathematical Biosciences*, **136**, 1–20.
- Williams, P.D., Day, T., Fletcher, Q. & Rowe, L. (2006) The shaping of senescence in the wild. *Trends in Ecology & Evolution*, **21**, 458–463.
- Williams, B.K. & Johnson, F.A. (1995) Adaptive management and the regulation of waterfowl harvests. *Wildlife Society Bulletin*, **23**, 430–436.
- Williams, B.K., Johnson, F.A. & Wilkins, K. (1996) Uncertainty and the adaptive management of waterfowl harvests. *Journal of Wildlife Management*, **60**, 223–232.
- Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002) *Analysis and Management of Animal Populations*. Academic Press, San Diego, CA, USA.
- Wilson, G.J. & Delahay, R.J. (2001) A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildlife Research*, **28**, 151–164.
- Wright, G.J., Peterson, R.O., Smith, D.W. & Lemke, T.O. (2006) Selection of northern Yellowstone elk by gray wolves and hunters. *Journal of Wildlife Management*, **70**, 1070–1078.
- Yee, T.W. (2010) The VGAM Package for Categorical Data Analysis. *Journal of Statistical Software*, **32**, 1–34.

Appendices

Appendix A Derivation of the Holling disc equation to partition search and handling time

The assumption made in Chapter 6 is that as the handling time needed to kill foxes is minimal, and that the search time for foxes is equal to the total time spent lamping over a time interval. However, if the handling time were greater, this could lead to biased results. Instead of making this assumption, it is possible to derive the Holling disc equation in the lamping context to explicitly partition the search time and handling time; with the caveat of either having to make an assumption about handling time or estimate it from data. Derivation of the disc equation also enables examination of the functional response of gamekeepers to foxes, i.e., the number of foxes killed over a time interval as a function of fox density.

Such a derivation continues from Eq. 6.7 by assuming that the gamekeeper attempts to kill all foxes seen, so the number of sightings Y over a time interval (time subscripts are removed from equations in this Appendix for clarity) is also the number of foxes that get shot at. However, the gamekeeper may be successful in killing only some proportion of the foxes seen with probability k , so the number of foxes killed C is:

$$C = kY = kdE_s N \quad \text{Eq. A.1}$$

where E_s is search time. When all foxes that are seen are killed, i.e., if the gamekeeper has perfect conditions for making a shot and is an expert marksman, then k will equal 1. From the FMS data, British gamekeepers kill on average only about 30% of the foxes seen. Given that the sighting probability is estimated to be about 0.5, the lamping efficiency (efficiency = sighting probability \times killing probability) is therefore 0.15, i.e., only 15% of foxes present on an estate will be killed during one complete pass of the estate area.

The next step is to separate the total time spent lamping E_a into two defined components i) time spent searching for foxes E_s , and ii) time spent killing and collecting

dead foxes, i.e., the handling time E_h per fox. This will allow an expression for the time spent searching to be found in terms of both the total time available for lamping and the handling time. As the gamekeeper spends more time killing foxes, less time is available to be allocated to searching for other foxes. This trade-off in time allocation can be expressed as:

$$E_s = E_a - E_h C \quad \text{Eq. A.2}$$

Note that by this definition the total time lamping is simply partitioned into time spent searching and time spent killing foxes, where the handling time is proportional to the number of kills. By substituting in Eq. A.1, this can also be written as:

$$E_s = E_a - E_h k Y \quad \text{Eq. A.3}$$

Substituting E_s from Eq. A.3 into Eq. 6.7 for sighting effort gives a new equation for the number of foxes seen over a time interval per total time available (rather than just search time which ignores the handling time):

$$Y = dN(E_a - E_h k Y) \quad \text{Eq. A.4}$$

To complete the derivation this needs to be solved for Y :

$$Y = dE_a N / (1 + kdE_h N) \quad \text{Eq. A.5}$$

This equation is the same as the Holling disc equation (Holling 1959a; b, 1965) which has been widely used in ecology to describe the functional responses of predators to their prey and to predict catch rates of prey by predators. It should be noted that Eq. A.5 collapses to Eq. 6.7 when E_h goes to zero; it is this property that allows the assumption that search time is equal to total time.

Appendix B Examination of the disc equation constant density assumption

A key assumption made in the disc equation derivation in Appendix A is that the mean fox density N along the gamekeepers search path remains constant over the total search time considered, thus implicitly assuming that the area searched a does not exceed the total area available, i.e., the estate area A . For models using differential equations with very small time intervals this is valid. Problems may be caused when using discrete time models, if the total search time means that the area searched over a time interval can exceed the estate area. In such situations, careful adjustment of the equations is required as foxes killed on the first pass through the estate will mean that the fox density on the second pass through the area may be greatly reduced. When lamping on an estate, it is possible that a gamekeeper could search the entire estate area more than once over a time interval, especially if areas were repeatedly searched because foxes were seen but not killed and given that the time interval that sighting data are aggregated over for the model time step is a week, rather than a single night. If the search-removal process is very efficient the predicted number of foxes killed on each successive pass would be biased relative to the predicted number of foxes killed under the assumption of constant density.

The estimated lamping efficiency for foxes is about 0.15. This figure is quite low, suggesting that the bias from making the assumption that density remains constant between passes over an estate will be relatively small. However, it remains important to quantify this bias under different degrees of lamping efficiency. This can be achieved by modifying the disc equation derivation to account for situations where the area searched can be greater than the estate area, and by correcting the density for the foxes that were killed on previous passes across the estate. From a total amount of time available for lamping, some of this will be allocated to searching for foxes, and some will be allocated to handling time, the amount of which will be proportional to the number of foxes killed. Search time therefore increases with the size of the area searched, but is limited by the total time available and the handling time used.

For any given total time for lamping, there will therefore be a maximum time that can be available for searching. Where this search time means that a will exceed A , the time spent

searching when $a = A$ (or multiples of A) is given simply by the estate area divided by the search rate ($2rv$), with the remaining search time given as a function of total and handling times. By substituting Eq. 6.7 into Eq. A.3 and then rearranging, search time is expressed as:

$$E_s = \min\{A^*/2rv, E_a/(1 + kdE_hN)\} \quad \text{Eq. B.1}$$

As A^* can be any multiple of the estate area to account for several passes across the estate, this expression can be used to determine the search time for each pass across an estate, allowing the number of foxes seen, and hence killed, on each pass to be calculated and the density at the start of the next pass to be adjusted. The first element of Eq. B.1 deals with the case where the area searched is equal to the estate area, so substitution into Eq. A.1 will give the number of foxes killed on each complete pass. The second element gives the total search time, meaning the search time over the final incomplete pass can be calculated by summing the search time from previous complete passes and subtracting this value from the total. An expression for the number of foxes killed C during pass i is therefore given by:

$$C_i = \begin{cases} kpAN_i & a_i = A \\ kd \left[E_a / (1 + kdE_hN_0) - \sum_{j=1}^{i-1} E_{s_j} \right] N_i & a_i < A \end{cases} \quad \text{Eq. B.2}$$

where a is the area searched during pass i . Note that where there is only a single incomplete pass, the search time summation is equal to zero and Eq. B.2 collapses to Eq. A.1. The number of foxes killed on each pass will therefore be the minimum of the two elements in Eq. B.2. Fox density during pass i is either assumed to be constant between passes, or is assumed to decrease by the number of foxes killed on each complete pass:

$$N_i = N_{i-1} - C_{i-1}/A \quad \text{Eq. B.3}$$

This assumes that the remaining foxes do not rapidly redistribute themselves across the estate before the end of a complete pass; if this were the case the decrease in density would need to be continuous. This also assumes that detection probability remains constant between

passes. This assumption could potentially fail if foxes become scared on the first pass and hide on the second or subsequent passes. The effect of this was not examined.

The bias from making the assumption that density remains constant over a time interval was examined by using the R statistical software (R Core Team 2013) to simulate a search-removal process across an estate using the above equations. The results from Chapter 6 were used to guide the input parameter values for initial fox density (1 fox km⁻²), speed of travel (10 km h⁻¹) and field of view radius (0.2 km), giving a search rate of 4 km² hr⁻¹ and, assuming a sighting probability of 0.5, a rate of successful search of 2 foxes km⁻² hr⁻¹. Arbitrary values were set for estate area (5 km²), total time available for lamping per week (10 hr), and a non-zero handling time (0.2 hr fox⁻¹). Alternate values of sighting probability (0.2, 0.5, 0.8) and killing probability (0.3, 0.6) were used to explore how lamping efficiency affected the potential bias.

Given these input parameter values, the number of foxes killed as a function of area searched over a time interval can be seen in Figure B.1 for differing levels of lamping efficiency. The number of foxes killed increases with area searched up until the estate area has been covered about 8 times, before an asymptote is reached due to the search time being exhausted. The bias increases with the area searched and with the lamping efficiency as expected. Bias in the number of foxes killed was assessed using per cent relative bias: PRB = 100 (C* - C) / C, (White *et al.* 1982) where C* is the number killed under the constant density assumption. Under a relatively low lamping efficiency (0.06, Figure B.1a) the maximum PRB was only 5.2%, while under a higher level of lamping efficiency (0.48, Figure B.1f) the maximum PRB was 46.4%.

For the scenario most likely relevant to the FMS data, with a lamping efficiency of 0.15 (Figure B.1c), the maximum PRB was 13.0%. This only became greater than 10% (representing a difference in number killed of <0.25 foxes) during the third search of the estate. The input parameters for estate area and total time available greatly affect the relationship, as if an estate is large and there are few hours available for lamping the potential for covering the estate more than once is small and the bias will be low. From the FMS data (Chapter 2), the mean value for estate area was 7.1 km² and the mean number of

hours lamping per week, of weeks in which lamping occurred, was 3.9 hr, meaning the average estate was larger and the average gamekeeper did less lamping per week than the values used in these simulations. Under these input parameters and a lamping efficiency of 0.15 only two complete searches were possible and the maximum PRB was 6.3%.

The use of the Holling disc equation has been questioned because the population density must be assumed to be constant, which is not true in population control contexts as the density is decreasing (Hone 1994). However, from these results it can be concluded that the bias from making the constant fox density assumption is low on the average estate. There are other functional response models (Rogers 1972; Fujii, Holling & Mace 1986; Tome 1988). Of these, the random predator model (Rogers 1972) accounts for decreasing density. Therefore, if the bias was found to be great a different model could be used, but this model relies on other assumptions that may not necessarily hold. In any case, if the efficiency is low enough – as is seemingly the case for foxes – the various models will be indistinguishable (Hone 1994).

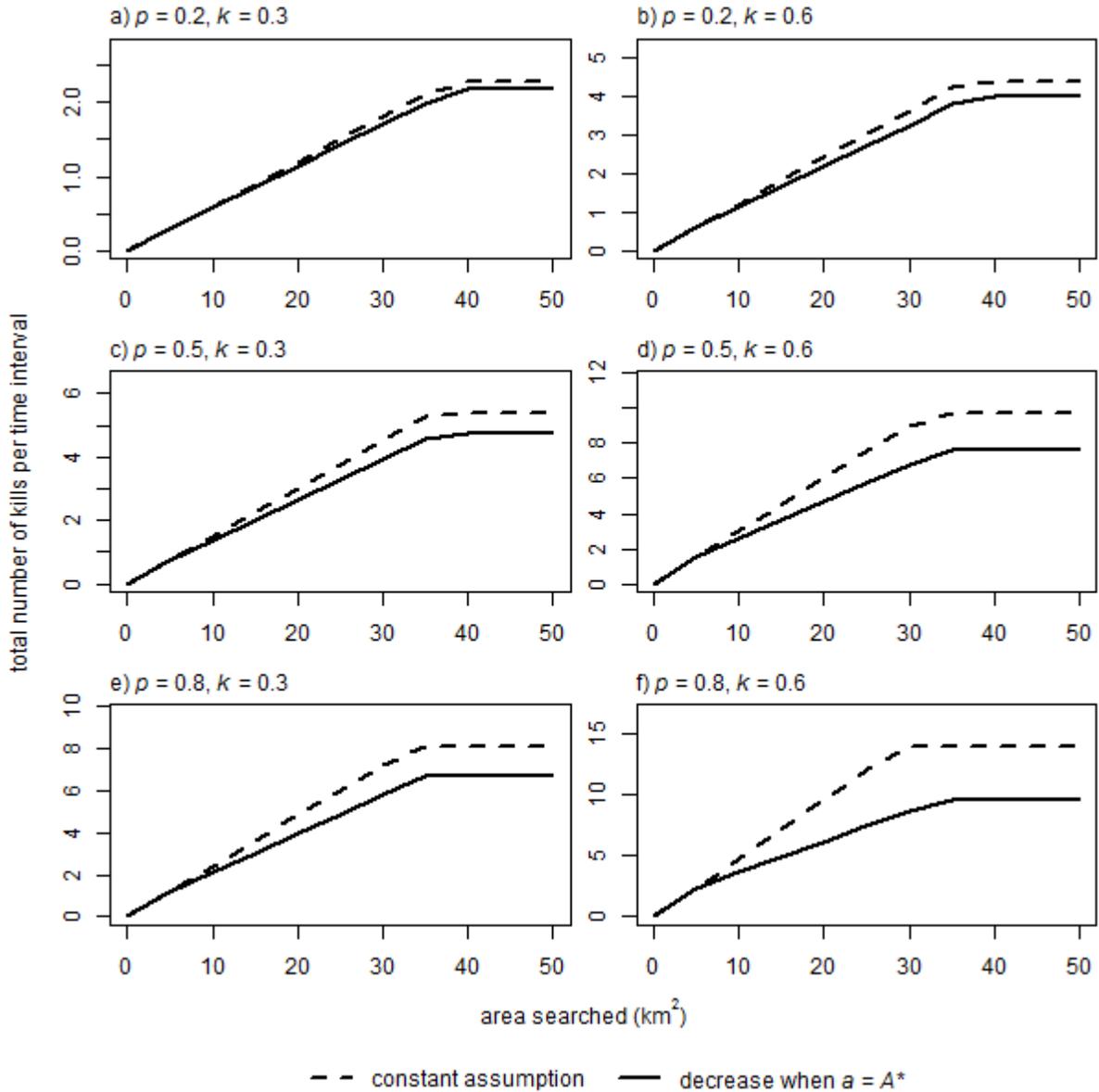


Figure B.1. Relationship between the total number of foxes killed on a 5 km² estate (area A) and the area searched (area a) showing the bias at each successive pass of A from making the assumption that fox density is constant over a time interval compared to if fox density at the start of each pass is reduced by the number of foxes killed on the previous pass. See text for input parameters. Each panel (a-f) shows the effect of differing levels of laming efficiency [sighting probability (p) \times killing probability (k)]. Panel c) is the scenario most likely relevant to the FMS data (* indicates that the decrease in density occurs at multiples of A)

Appendix C Sequential searching through habitats of differing preference

The Holling disc equation also makes the assumption that foxes are randomly distributed over the search area. It is possible that this assumption may be invalid, as foxes can be expected to prefer particular habitat patches and spend more time in them under the optimal search rate hypothesis (Gendron & Staddon 1983). At the landscape scale in Britain, fox density varies with landscape type (Webbon, Baker & Harris 2004). At the territory scale, foxes generally prefer a mosaic patchwork of scrub, woodland and farmland habitats (Macdonald & Reynolds 2004). While a typical fox territory will usually contain more than one of the preferred habitat patches, foxes do not utilise each habitat type in the same way due to differing prey availability (Lloyd 1980). This habitat selection usually varies seasonally as different prey becomes available (Cavallini & Lovari 1991). Within a territory, foxes will therefore be expected to spend more time hunting in particular habitats, and that the ‘best’ territories will encompass these areas. This means that although the density on the estate will be a constant (prior to any foxes being killed), the density of foxes in a particular habitat within the estate during a search will be different to the density in other habitats, meaning that fox distribution across the estate is not random at any given time during the search.

Foxes are primarily nocturnal, with activity usually beginning about an hour after dusk and ending an hour before dawn, often with an inactive period during the middle of the night (Reynolds & Tapper 1995a). Foxes show regular feeding habits and have been found to perform similar patterns of movement through their territory each night (Lloyd 1980). Given this, it is reasonable to assume that foxes will begin hunting each night in the habitat within their territory with the highest prey availability. Gamekeepers will usually base their lamping efforts upon previous experiences. They will begin lamping at a similar time to when foxes become active after dusk, partly because it is easier to sight foxes when they are moving compared to when they are lying up in cover, but also because they will want to get their evening of lamping finished and go home to bed. Gamekeepers usually have a fixed lamping route around an estate, which depends on the layout of tracks over the estate. However, another reasonable assumption is that a gamekeeper will start lamping in the area

on an estate where they have seen and killed the most foxes previously, and that this success depended upon both the density and sightability of foxes in that habitat. Given the constraints of the tracks, gamekeepers will then continue their search sequentially to the areas of decreasing success, which in turn reflect the habitats with decreasing fox density.

Such a search process can be visualised using Figure C.1 by assuming the gamekeeper has a lamping route along tracks that goes through habitats 1, 2, 3 and 4, and that the search begins in the highest density habitat (1), then moves into the next highest density habitat (2), and so on, before completing the route in the lowest density habitat (4) if there is enough search time available. Further modification can be made to the Holling disc equation derivation from Appendix B to incorporate this sequential search process, which can then be used to examine how a sequential search across multiple habitats with differing fox densities would affect the functional response between gamekeepers and foxes when compared to the assumption that fox density is random over a search area that is made up of a single habitat type.

If we take a search area A and look at n habitat areas A_i , ordered by densities N_i , and assume that these areas are searched in the order N_1, N_2, \dots, N_n , then the search time for each area i is given by:

$$E_{s_i} = \min\{A_i/2rv, E_{a_i}/(1 + kdE_h N_i)\} \quad \text{Eq. C.1}$$

where E_{a_i} is the total time remaining when the gamekeeper arrives at area i . The total time remaining is obtained by subtracting the sum of search and handling times used before arrival at area i from the total time available:

$$E_{a_i} = E_a - \sum_{j=1}^{i-1} A_j/2rv - \sum_{j=1}^{i-1} E_h C_j \quad \text{Eq. C.2}$$

where the number of foxes killed in areas j searched completely before reaching area i is given by:

$$C_j = kpA_jN_j \quad \text{Eq. C.3}$$

The number of foxes killed in the last searched area i is given by Eq. A.1, where the search time and density relate to those for area i . These equations can be further modified to incorporate multiple passes across the estate; the details are not shown here.

A simplistic multiple habitat estate is shown in Figure C.1, and contains four different habitat types (1-4). It is assumed that each habitat is searched completely, before the search moves sequentially onto the next habitat type. The gamekeeper starts in the habitat with the highest density first, even if that area is small. The area of each of the habitat types in Figure C.1 increases in size ($1.5 \rightarrow 2.5 \rightarrow 3 \rightarrow 3 \text{ km}^2$), as the fox density in each habitat type decreases. The estate is assumed to have an overall fox density of 1 fox km^{-2} . Based upon this density, the foxes were redistributed within each habitat type based upon the weightings ($\times 4 \rightarrow \times 2 \rightarrow \times 1 \rightarrow \times 0.5$). The same input parameters were used as in Appendix B, except that the total total time available was 1 hour. The search progressed from habitat 1 until the time available was used up. If the time available is very short, then the gamekeeper will only have time to search the higher density habitats.

Figure C.2 shows that the number of foxes killed is higher for a given fox density in the multiple habitat scenario. This is because the gamekeeper will encounter habitats with higher fox density earlier in the search compared to the single habitat scenario; at very high densities the difference decreases due to the limitation of handling time. At the densities at which foxes are found in Britain, this means there is a large difference in the number of foxes killed from making the random search assumption. At a 1 fox per km^2 density, the difference in the number of foxes killed over a time interval is 0.54 foxes (single) compared to 1.06 foxes (multiple), while at a 2 fox per km^2 density, the difference is 0.97 foxes (single) to 1.91 foxes (multiple). At these densities, this indicates that a search process through a multiple habitat estate is almost 100% more efficient than if the single habitat assumption is made.

If foxes are not distributed randomly within multiple habitats and gamekeepers do search sequentially such as this, the potential bias from making the randomly distributed assumption is therefore large. However, the habitats along a gamekeeper's search path along

tracks on an estate are often more complex than the simplistic example here. Although the gamekeeper might start lamping in the area where they have previously had most success killing foxes, where a gamekeeper follows a farm track the next habitat encountered may instead be one of much lower fox density rather than the next lowest, as e.g., the track may follow the field margins of different crop types and go alongside different patches of woodland, meaning that a sequential search is not possible. There is also the possibility that those areas where there has previously been most success are more closely related to the sightability of foxes than to fox density itself. In any case, applying a multi-habitat model to the FMS data used in this thesis is not feasible as there are insufficient details on the habitats within an estate and where foxes were killed; such detail would be necessary to estimate habitat-dependent density.

A further issue with the multi-habitat scenario concerns the process by which foxes redistribute themselves following a number being killed during a search. If there is only one complete pass, it is assumed that foxes do not rapidly expand into any newly available territories during the search time and that the density across the estate is a constant until the end of the pass. If there are multiple passes over a time interval, it is assumed that the remaining foxes redistribute themselves in a density-independent way within the territory structure so that the distribution of foxes across the estate before the start of the next pass can be considered random. While this assumption seems reasonable for a single habitat estate, such density-independent redistribution is unlikely for multiple passes across a multi-habitat estate. Instead, foxes in the poorer habitat types are likely to preferentially move into the better habitats in some density-related way. This will be exacerbated on large estates where a complete pass may take a long time, allowing more time for foxes to move around between habitats. This density-related redistribution of foxes in a multi-pass scenario would need to be addressed before such a multi-habitat model for foxes was further examined.

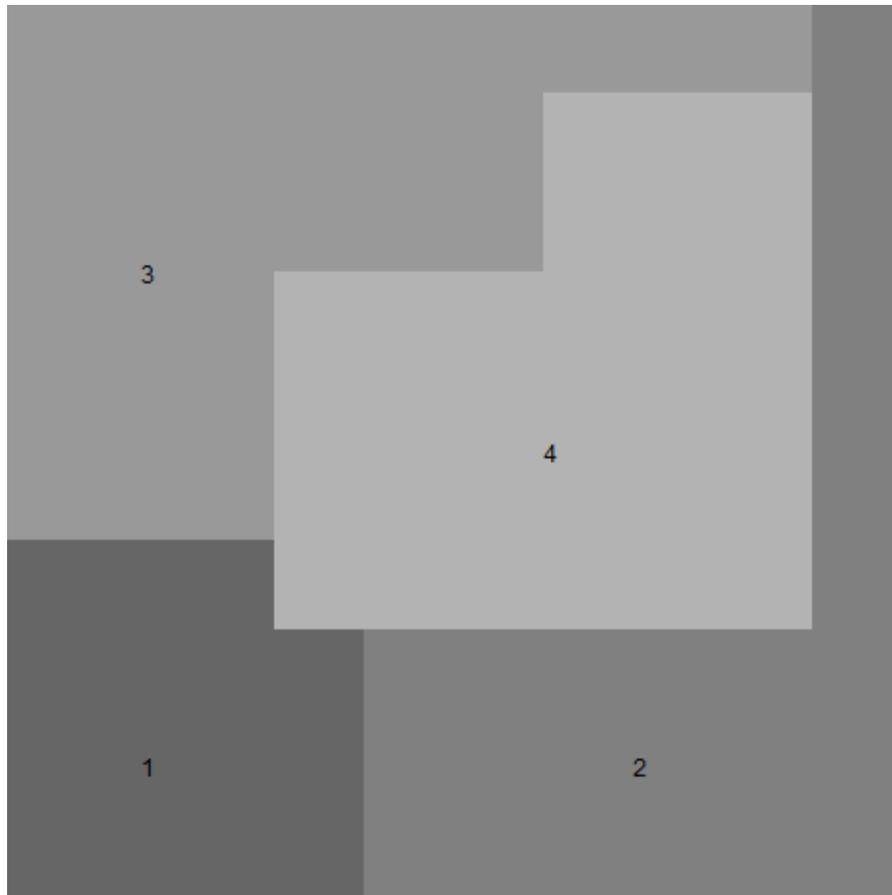


Figure C.1. A hypothetical estate of 10 km², divided into 10 ha blocks, comprised of different habitat types (numbered 1-4) which have increasing size (1.5 km², 2.5 km², 3 km², 3 km²). Each habitat type contains different numbers of foxes (weighted: ×4, ×2, ×1, ×0.5) based upon decreasing prey availability in a given season. Gamekeepers are assumed to start in the area of highest fox density (1) and search sequentially through each habitat type, searching the area of lowest fox density (4) last.

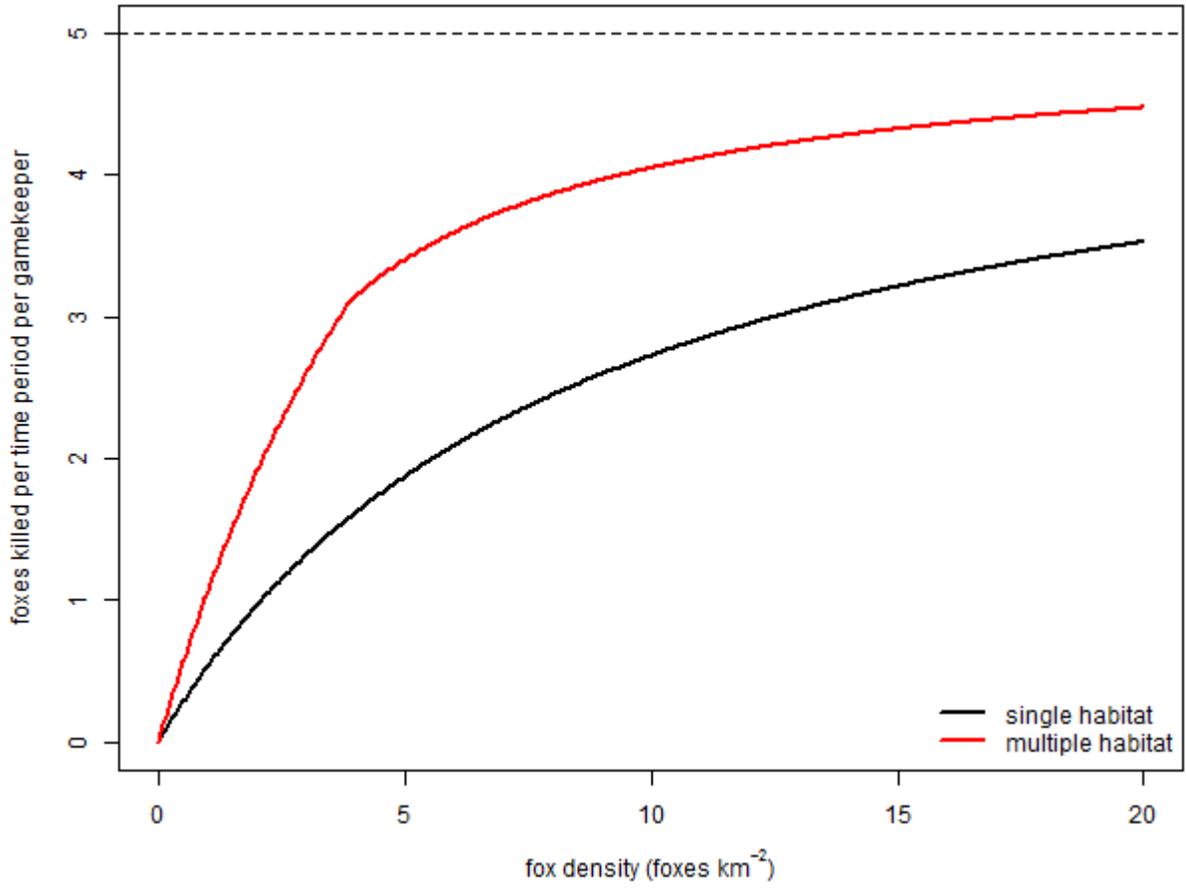


Figure C.2. Functional response of gamekeepers to foxes depending upon the assumptions made about the habitat types within the estate being searched over.

Appendix D Development of an informative prior for per capita birth rate

D.1 Introduction

There is a biological limit on the number of cubs a female red fox can conceive, so in a Bayesian population dynamics model it is reasonable to specify an informative prior probability distribution for the maximum *per capita* annual birth rate r that limits the joint-posterior parameter space to biologically realistic values. Assuming that births are density-dependent, maximum *per capita* birth rates should be observed in fox populations that are at very low densities, e.g., those populations suppressed by high culling mortality. This assumption is supported by observations that larger litter sizes occur in regions subject to heavy culling pressure compared to regions with lower culling mortality (Heydon & Reynolds 2000b).

Per capita birth rate can be determined from litter size per female data if an assumption is made about the male to female sex ratio in the population. Adult foxes are territorial and the basic social unit is a monogamous pair, although in higher density populations extended social groups are formed in which a dominant pair tolerate several related subordinate females (Macdonald 1979; Reynolds & Tapper 1995a; Macdonald & Reynolds 2004). In high density populations the subordinate females are usually non-productive due to high levels of interaction with the dominant female, while in low density populations these females can instead find empty territories in which to disperse into and breed successfully (Macdonald 1980b). Populations subject to high levels of culling mortality therefore have a low proportion of non-productive females (Lloyd 1980). From this, a reasonable assumption is that the male to female sex ratio is 50:50, meaning that maximum *per capita* birth rate can be approximated by dividing the litter size per female from a heavily culled population in half.

The maximum litter size reported in the literature is 12 cubs per female (Macdonald & Reynolds 2004), but it is not known how intensive the culling was in this population. Use of these data could lead to specification of a uniform prior for r that ranges from zero to an upper limit of six fox cubs *per capita*. However, a uniform prior is only vaguely informative

as equal weight is given to the values at the extremes of the distribution as to those in the centre. Litter sizes in rural Britain are usually in the range of four to six cubs per female and extreme values (>10 cubs in a litter) are not very common, even in suppressed populations (Voigt & Macdonald 1984; Heydon & Reynolds 2000b; Macdonald & Reynolds 2004).

A more informative prior probability distribution would show variation around the central tendency of litter size data obtained from heavily culled populations. Heydon & Reynolds (2000b) studied three largely rural regions of Britain (mid-Wales, east Midlands, East Anglia) and found that fox population density was suppressed by higher culling mortality in two of these regions. Litter sizes were significantly greater in these regions (mid-Wales and East Anglia) compared to a region where culling mortality was lower (east Midlands). The mean and variance of litter sizes from the populations with heavy culling were used together with Fox Monitoring Scheme (FMS) data on litter sizes from estates where foxes were being culled to parameterise an informative prior probability distribution for maximum *per capita* birth rate.

D.2 Methods

All estimated litter sizes per female were determined from counts of dark placental scars from females killed during the March to July period (Lindström 1981). Litter size estimates were not adjusted for non-productive females because none were found in the heavily culled samples from the mid-Wales and East Anglia (Heydon & Reynolds 2000b), supporting the assumption of a 50:50 sex ratio. The mean annual litter sizes per female were $6.38 \text{ cubs} \pm 0.41$ in mid-Wales, and $6.24 \text{ cubs} \pm 0.35$ in East Anglia (\pm s.e.), from regional samples of 21 and 45 female foxes, respectively (Heydon & Reynolds 2000b). The standard deviations in sampled litter sizes were calculated from the standard error of the means using these sample sizes, giving values of 1.88 cubs (mid-Wales) and 2.35 cubs (East Anglia).

As r can take non-integer values it should be characterised by a continuous distribution, so although females can only have discrete litter sizes, the litter size data were assumed to be drawn from a gamma distribution to allow later conversion to *per capita* litter sizes following an assumption of a 50:50 male to female sex ratio. Also, given that the variances in litter size samples were less than the means, the discrete Poisson or negative

binomial distributions are unsuitable. The parameters of the gamma distribution were calculated using the mean and variance in litter size samples from each region (Evans, Hastings & Peacock 2000). These regional gamma distributions were used to generate 500 random numbers to give simulated litter size data that had the same mean and variance as the regional samples. Next, given a 50:50 sex ratio assumption, values from the two simulated datasets were pooled across regions and then divided by two to give a *per capita* litter size dataset that would be gamma distributed.

The maximum likelihood estimates (MLE) of the gamma distribution parameters were obtained from the simulated *per capita* litter size data using the ‘fitdistr’ function in the MASS package (Venables & Ripley 2002) of the R statistical software (R Core Team 2013). The maximum likelihood estimates were almost identical to the analytically calculated values, but using a numerical approach to estimation allowed the standard errors of the estimates to be obtained from the information matrix. These were required in a later step in the analysis. The fitted gamma distribution was tested for goodness-of-fit to the simulated *per capita* litter size data using the Kolmogorov-Smirnov test.

The *per capita* litter size distribution obtained by this approach was then used as a prior in an analysis that used the FMS litter size data to obtain a posterior predictive distribution for r . As this distribution reflects the uncertainty in r it can be used as an informative prior for this parameter in a Bayesian population dynamics model. The analysis assumed that the FMS litter size data were from populations with 50:50 sex ratios and were drawn from a gamma distribution:

$$x_i \sim \text{gamma}(a, b)$$

where x are the *per capita* litter size values and a and b are priors for the shape and rate parameters. As a and b can only take positive values, the priors were assumed to take censored normal distributions that had a lower bound at zero to prevent numerical sampling problems. The priors were:

$$a \sim \text{Normal}(\mu_a, \tau_a)$$

$$b \sim \text{Normal}(\mu_b, \tau_b)$$

Where μ_a and μ_b are the MLE of the shape and rate parameters, respectively, and τ_a and τ_b are the inverse of the variance calculated from the standard errors of these estimates. The posterior predictive distribution for r was obtained by specifying a gamma distribution using the posteriors for the shape and rate parameters.

All Bayesian analysis was performed using WinBUGS (Spiegelhalter *et al.* 2007), implemented from within R using the R2WinBUGS package (Sturtz, Ligges & Gelman 2005). Samples of the posterior distribution of the parameters were obtained using Markov Chain Monte Carlo (MCMC) methods. Some parameters were slow to mix across the joint posterior space, so to reduce autocorrelation in the MCMC chains every tenth sample was recorded following removal of an initial burn-in of 10,000 samples. The posteriors were estimated from two independent chains of 20,000 samples. Convergence of the samples to the posterior distributions was assessed within R using the CODA package (Plummer *et al.* 2006) by examination of the Gelman-Rubin and the Geweke convergence diagnostics (Geweke 1992; Gelman *et al.* 2004).

D.3 Results

The shape parameters of the gamma distributions used to simulate data on regional litter size at birth per female were calculated as 11.53 (mid-Wales) and 7.06 (East Anglia), with the rate parameters calculated as 1.81 (mid-Wales) and 1.13 (East Anglia). The simulated regional distributions of litter size are shown in Figure D.1. The *per capita* litter size dataset obtained from these simulated data (Figure D.2) had a mean of $3.17 \text{ cub fox}^{-1}\text{yr}^{-1} \pm 1.07$ (s.d.). The CV of this distribution was 0.338.

The gamma distribution fitted to the *per capita* litter size data had a shape parameter MLE of 8.77 ± 12.20 (s.d.) and a rate parameter MLE of 2.76 ± 3.95 (s.d.). These estimates were equal to those obtained by analytically calculating them from the mean and variance of the data (Figure D.2). As the P -value from the Kolmogorov-Smirnov goodness-of-fit test was >0.05 the gamma distribution was determined to be suitable for these data.

A total of 65 foxes were autopsied from estates taking part in the FMS, and under the 50:50 sex ratio assumption these data had a mean *per capita* birth rate of $2.80 \text{ cub fox}^{-1}\text{yr}^{-1} \pm$

2.07 (s.d.). These data updated the prior of the gamma distribution parameters (Figure D.3), resulting in a posterior mean for the shape parameter of 7.655 ± 1.265 (s.d.) and a posterior mean for the rate parameter of 2.730 ± 0.464 (s.d.). The posterior predictive distribution for r (Figure D.4) had a mean of $2.818 \text{ cub fox}^{-1}\text{yr}^{-1}$ and a 95% credible interval of [1.158, 5.186]. The CV of this distribution was 0.368.

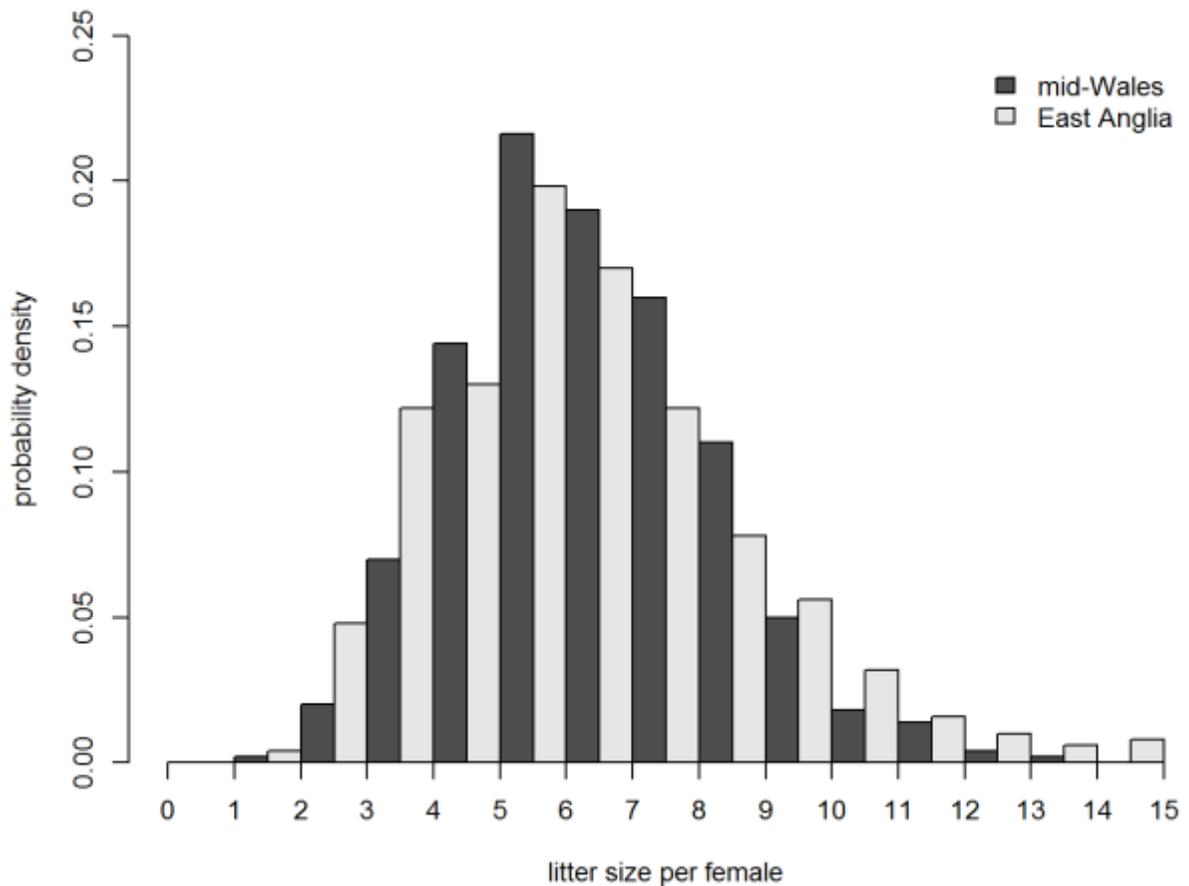


Figure D.1. Simulated litter size per female data from mid-Wales and East Anglia obtained by generating random numbers from a gamma distribution parameterised using the sample mean and standard deviation in litter size from each region. Data are shown binned into integer values.

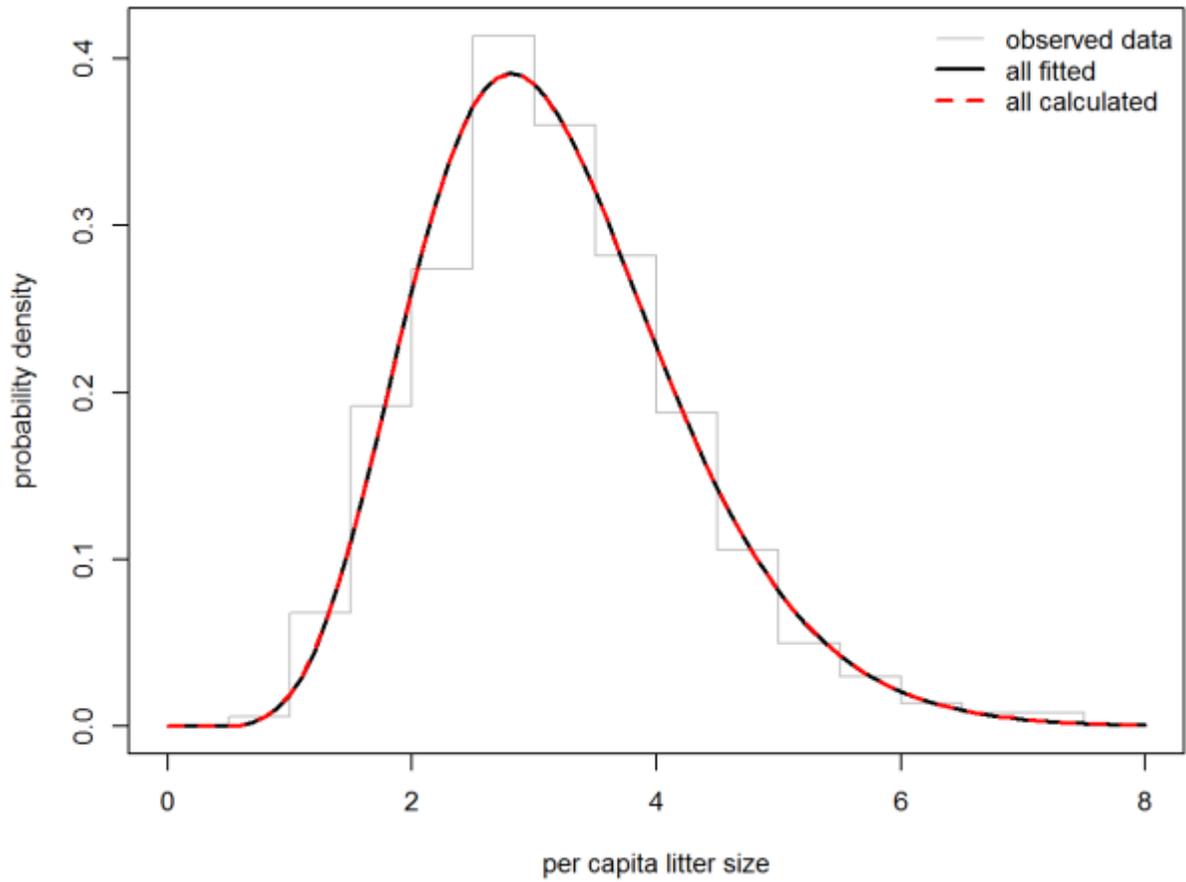


Figure D.2. Distribution of 'observed' *per capita* birth rate. Gamma probability density functions fitted to these data by maximum likelihood and by analytical calculation of the shape and rate parameters are shown for comparison.

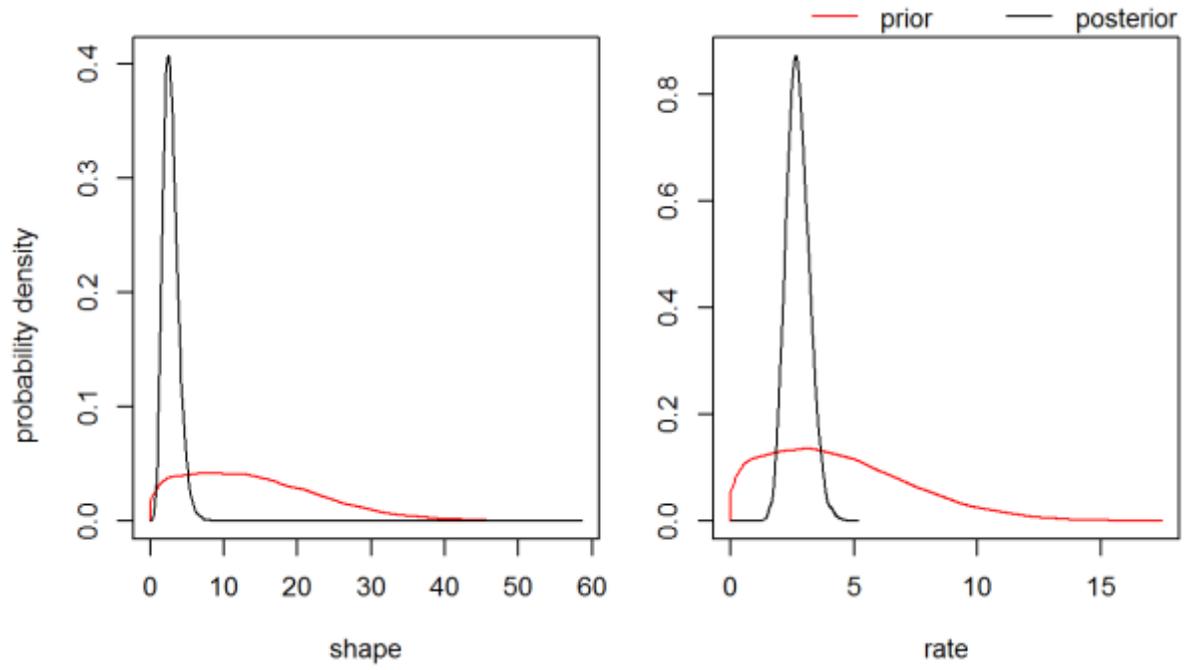


Figure D.3. Prior and posterior probability distributions for the shape and rate parameters of the gamma distribution.

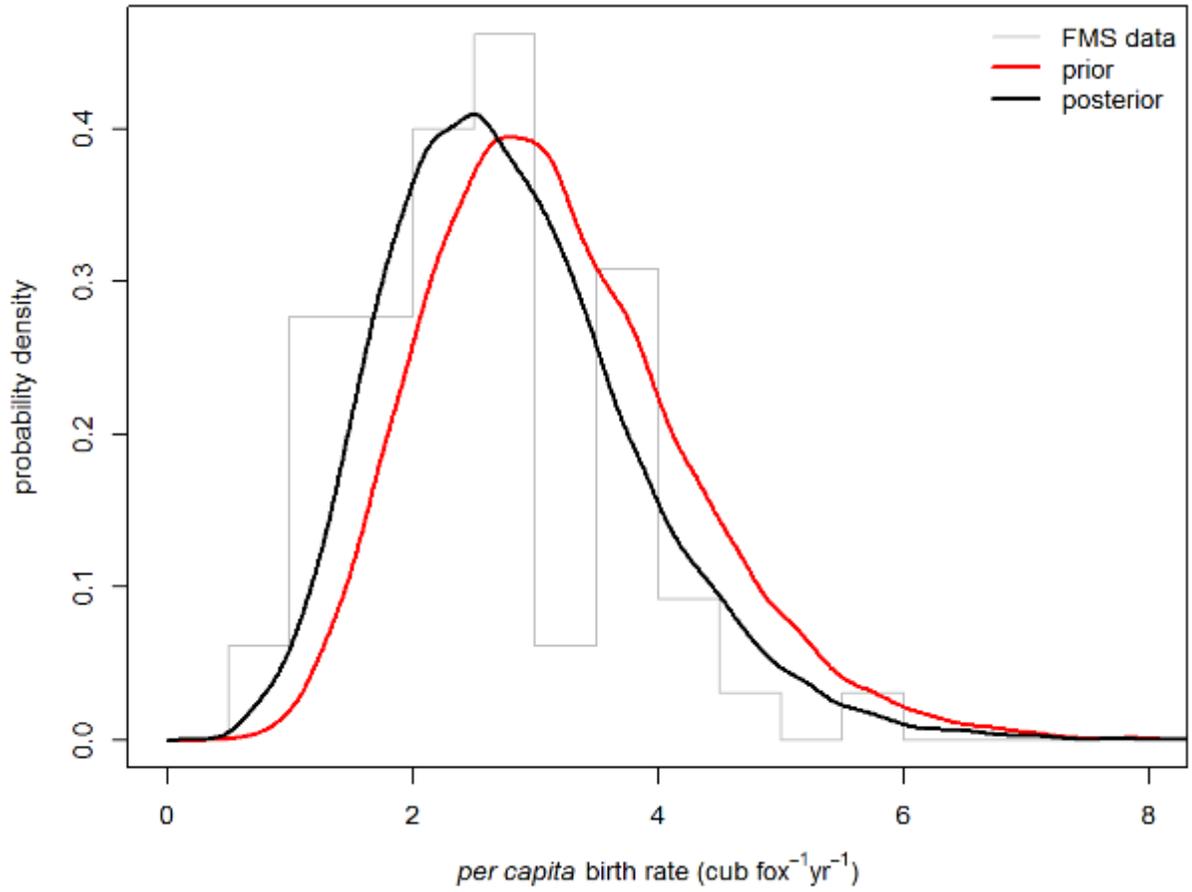


Figure D.4. Posterior predictive distribution for *per capita* birth rate specified by gamma distribution shape and rate parameters obtained by updating the prior with the FMS litter size data.

Appendix E Fox density and parameter estimates from modelled estates

This Appendix contains the posterior outputs from all modelled estates not included in the results section of Chapter 7, with figures in alphabetical order by estate code.

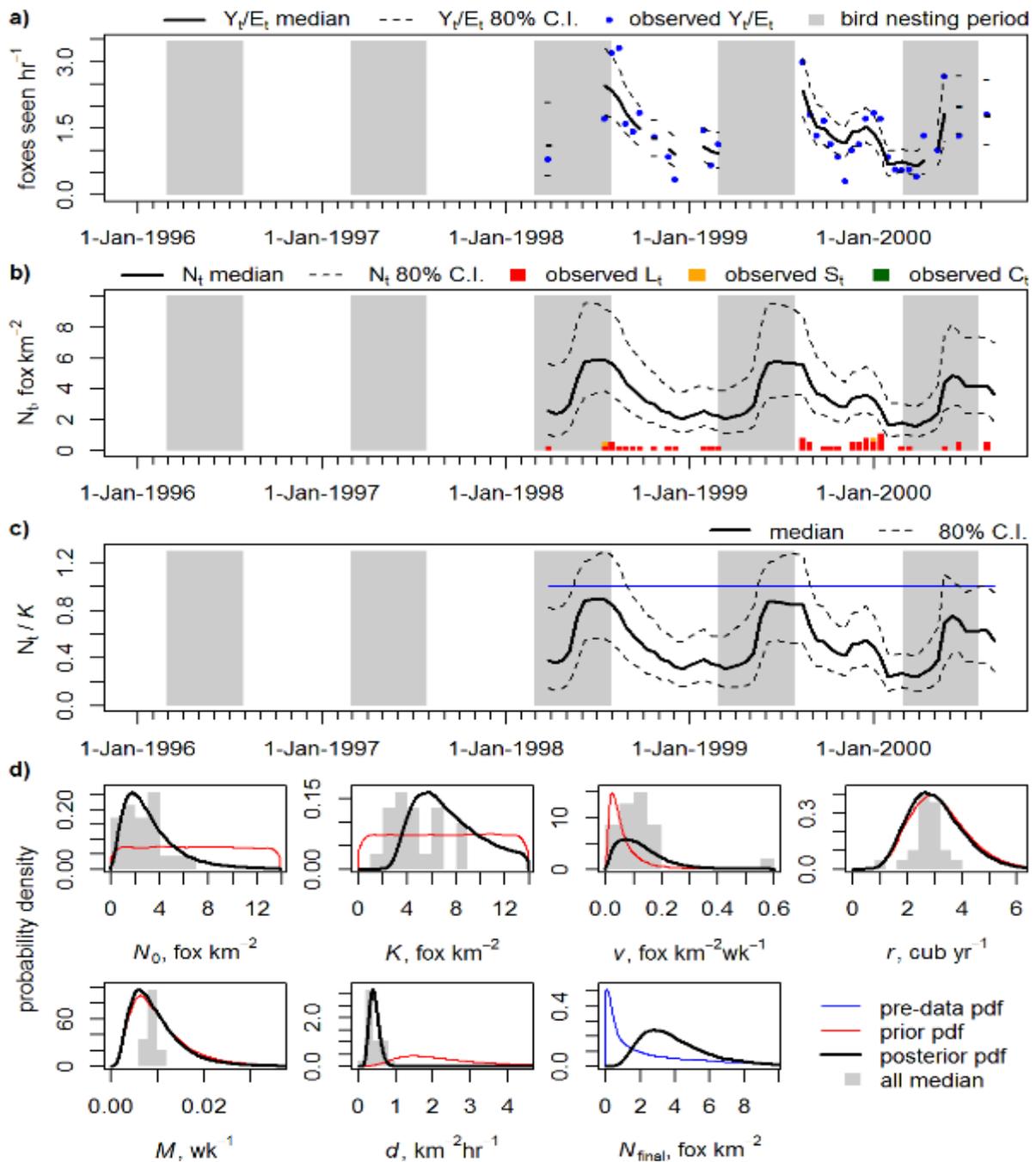


Figure E.1. Results for BMM showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a)-c) the bird nesting period is shown as a reference.

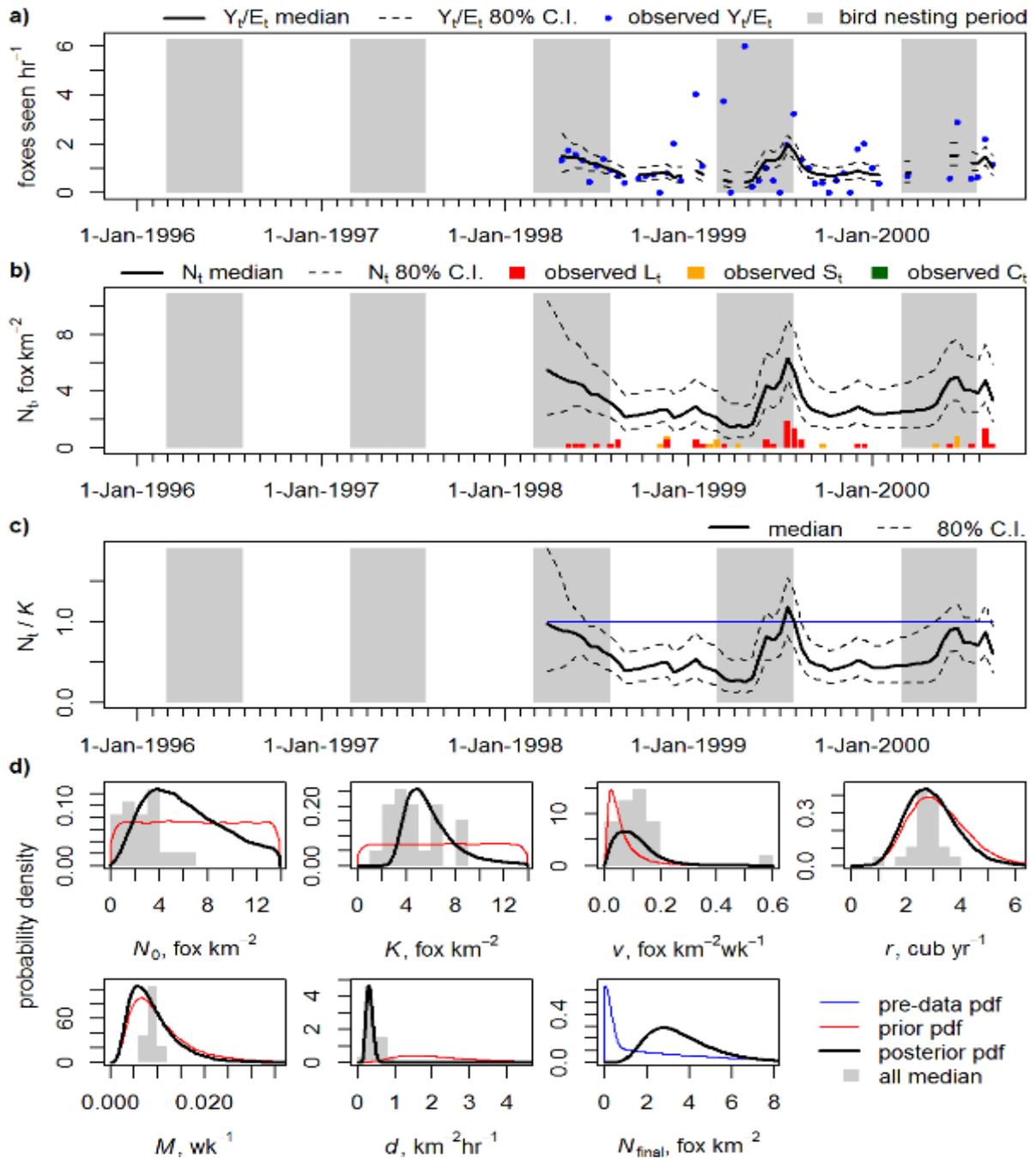


Figure E.2. Results for CHU showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

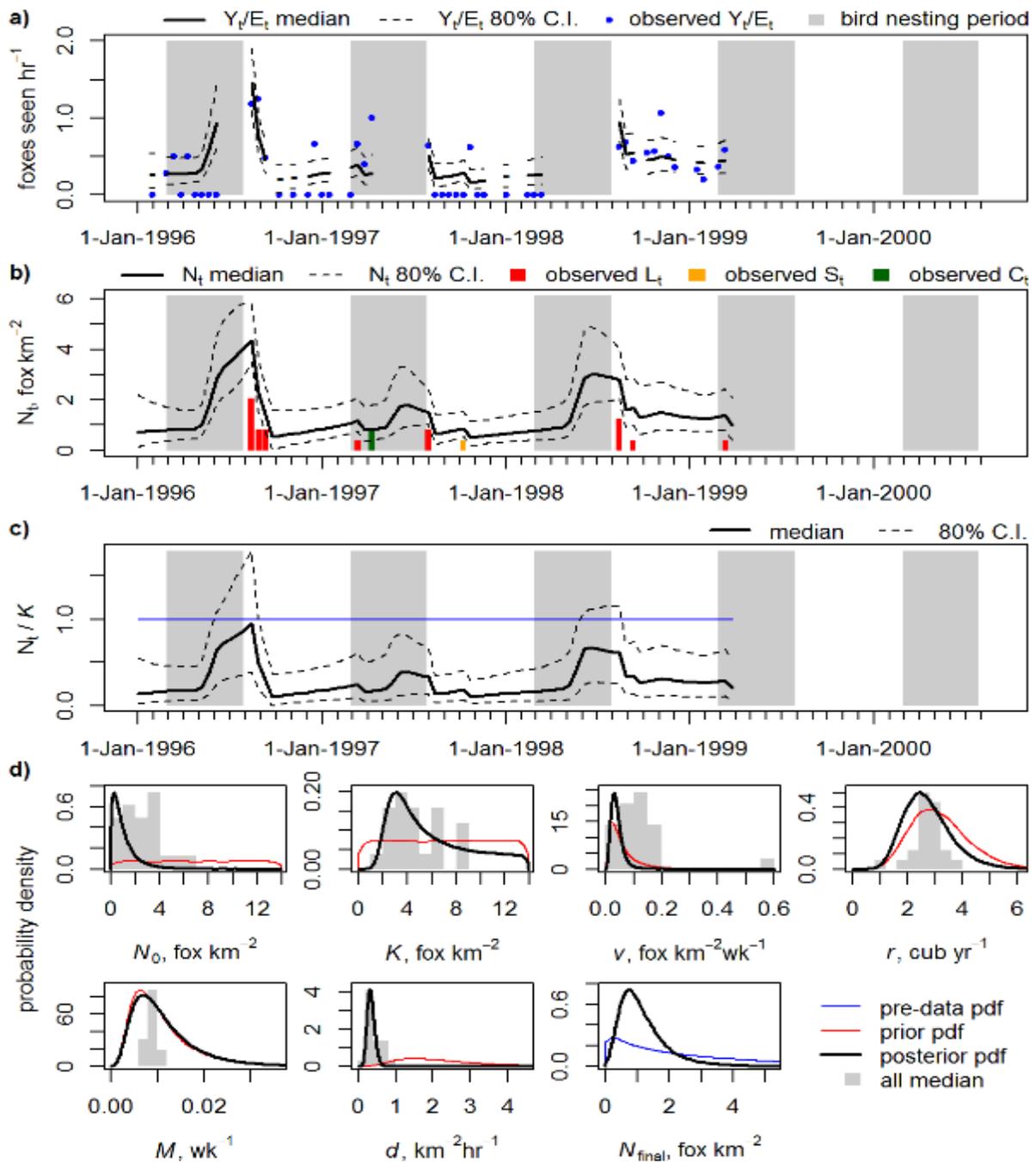


Figure E.3. Results for CIP showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

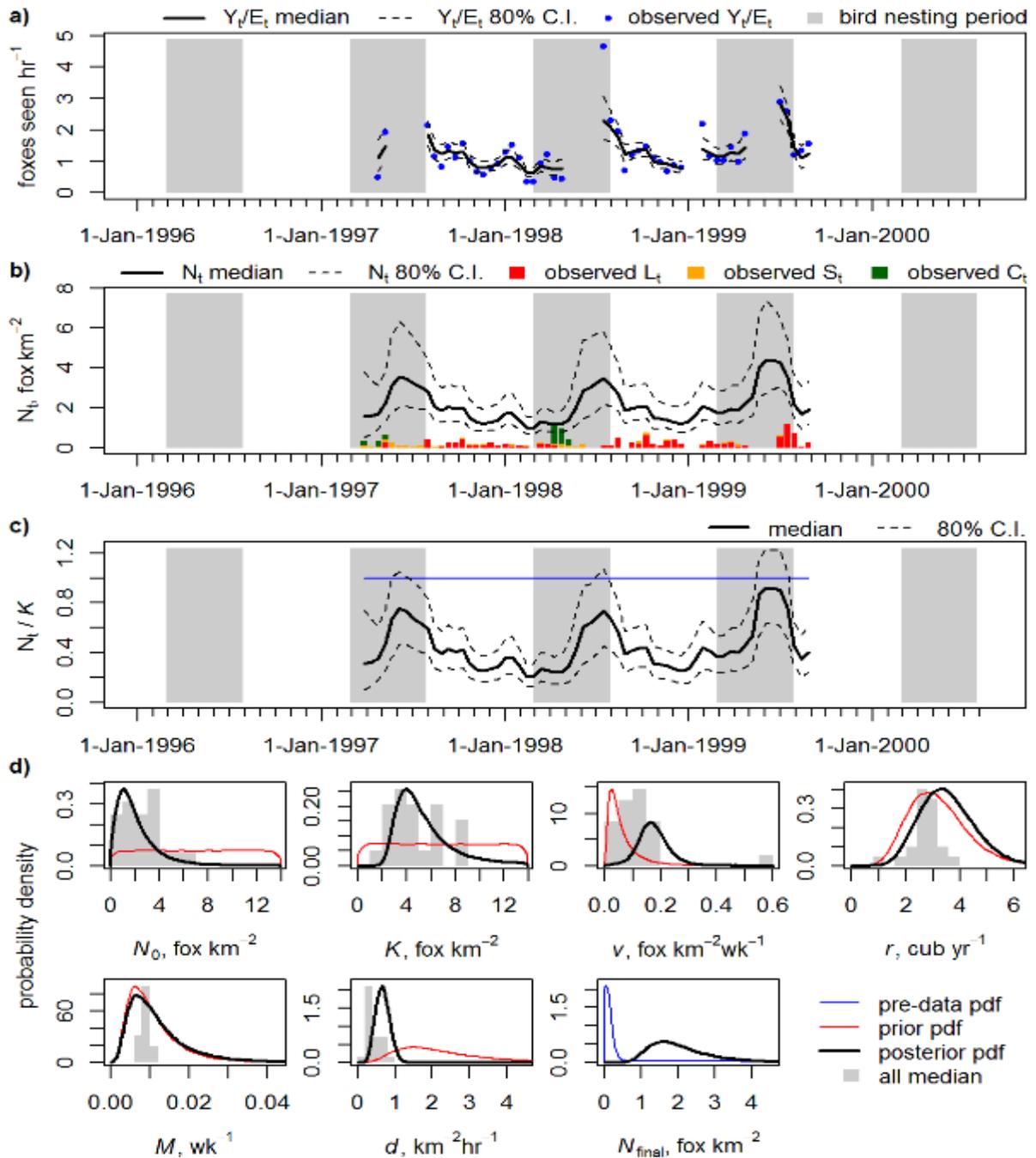


Figure E.4. Results for DWS showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

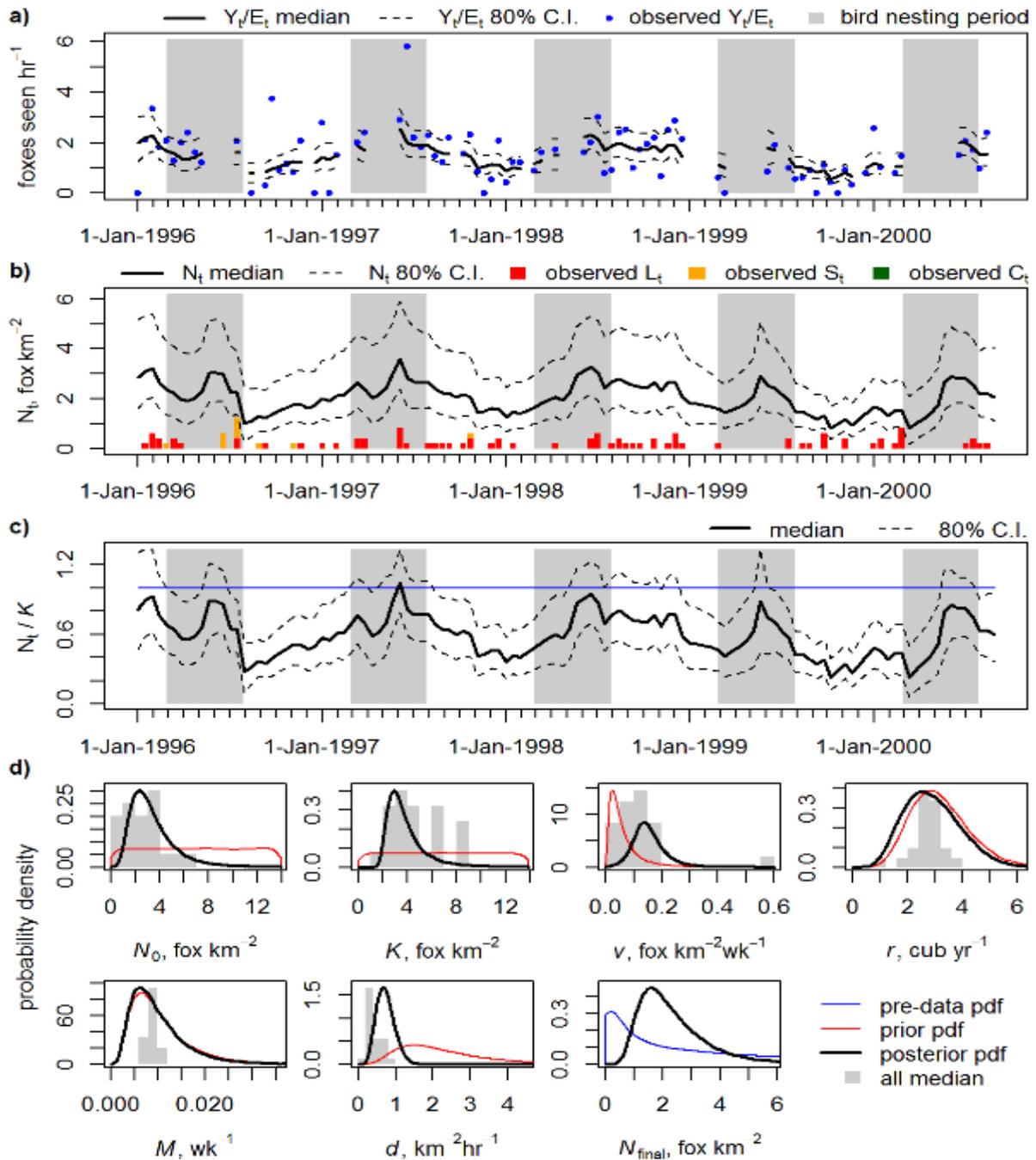


Figure E.5. Results for EWE showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

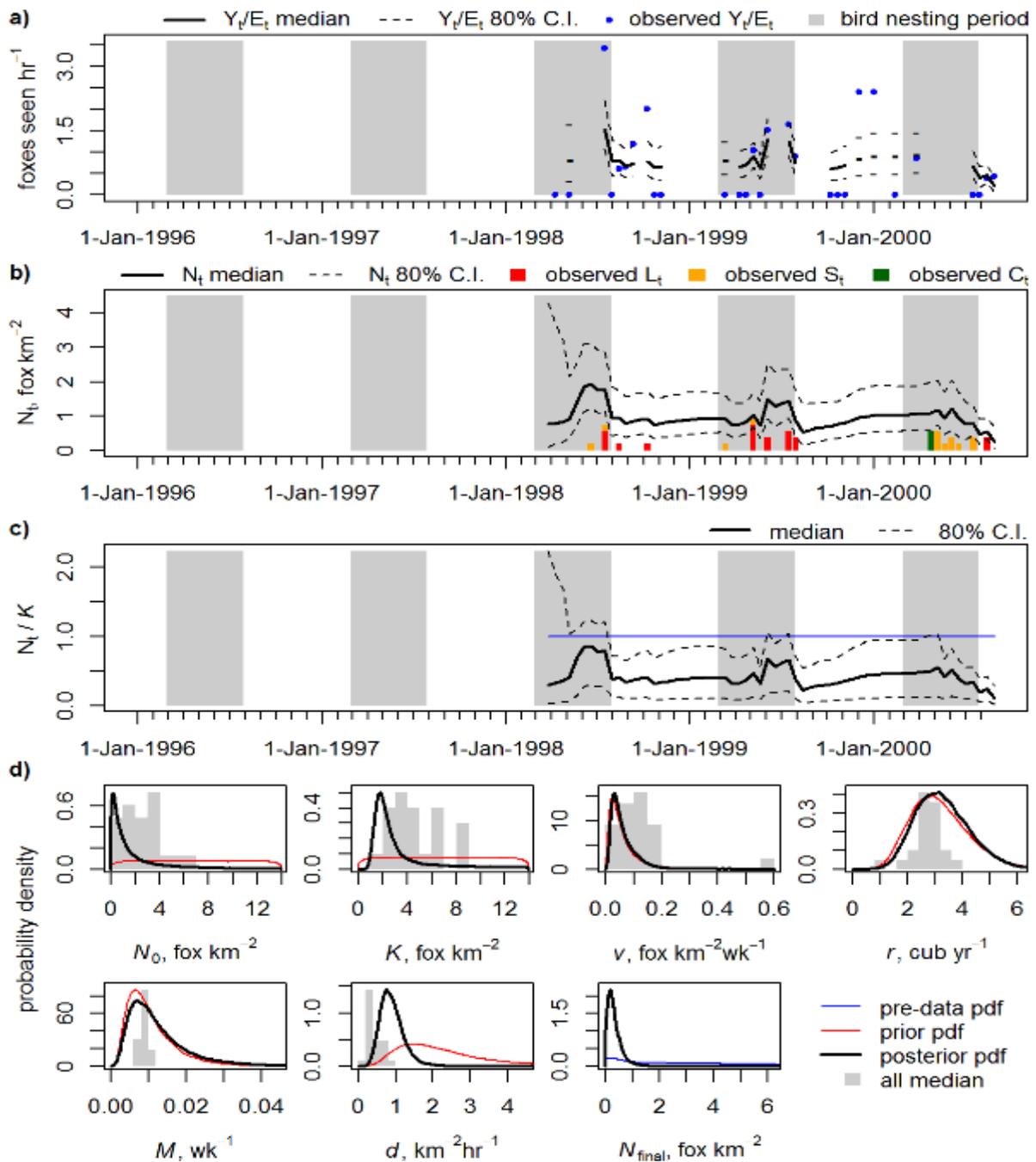


Figure E.6. Results for FAH showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

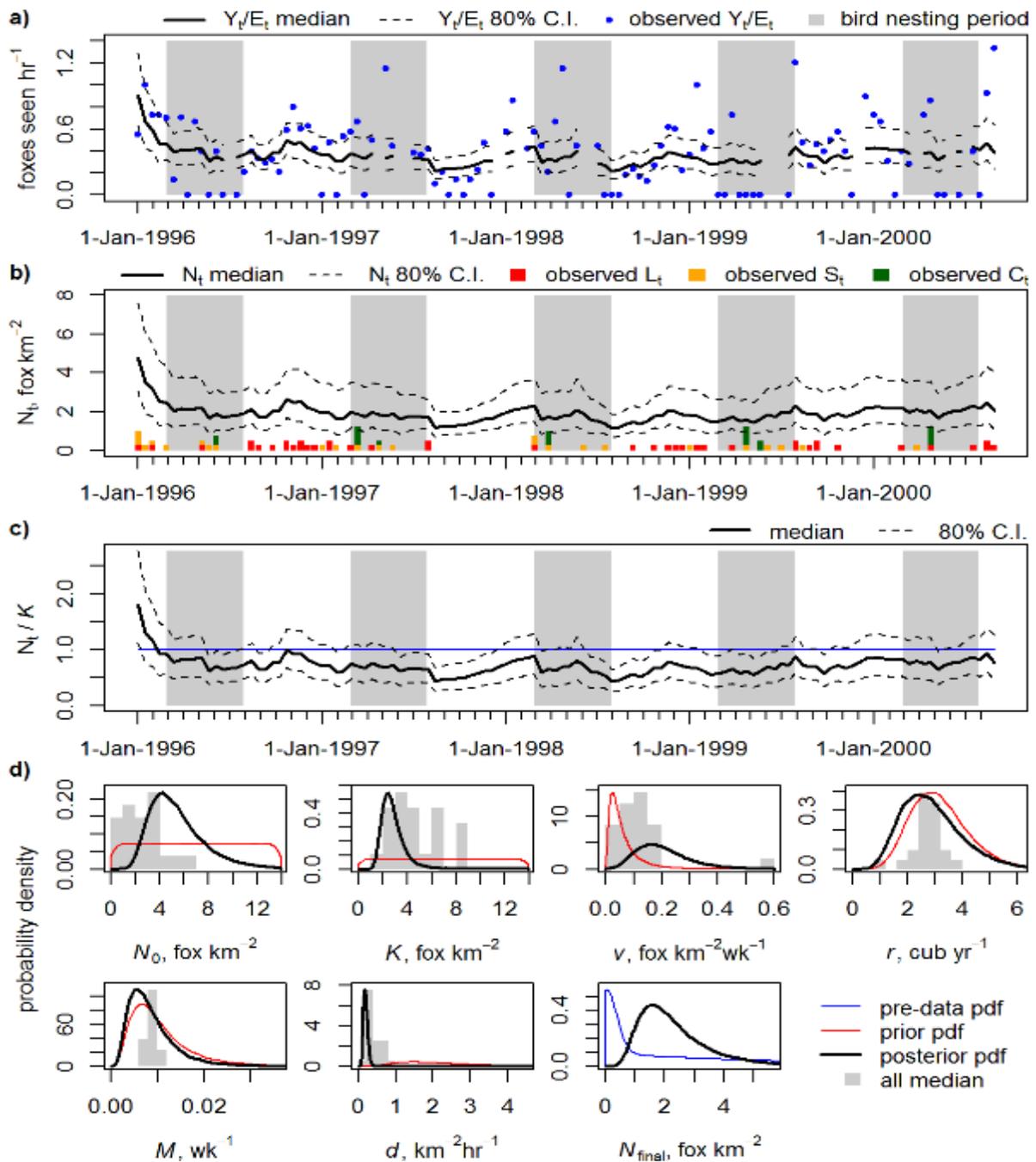


Figure E.7. Results for FHC showing a) posterior fit of the model to sighting rate (Y_i/E_i); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

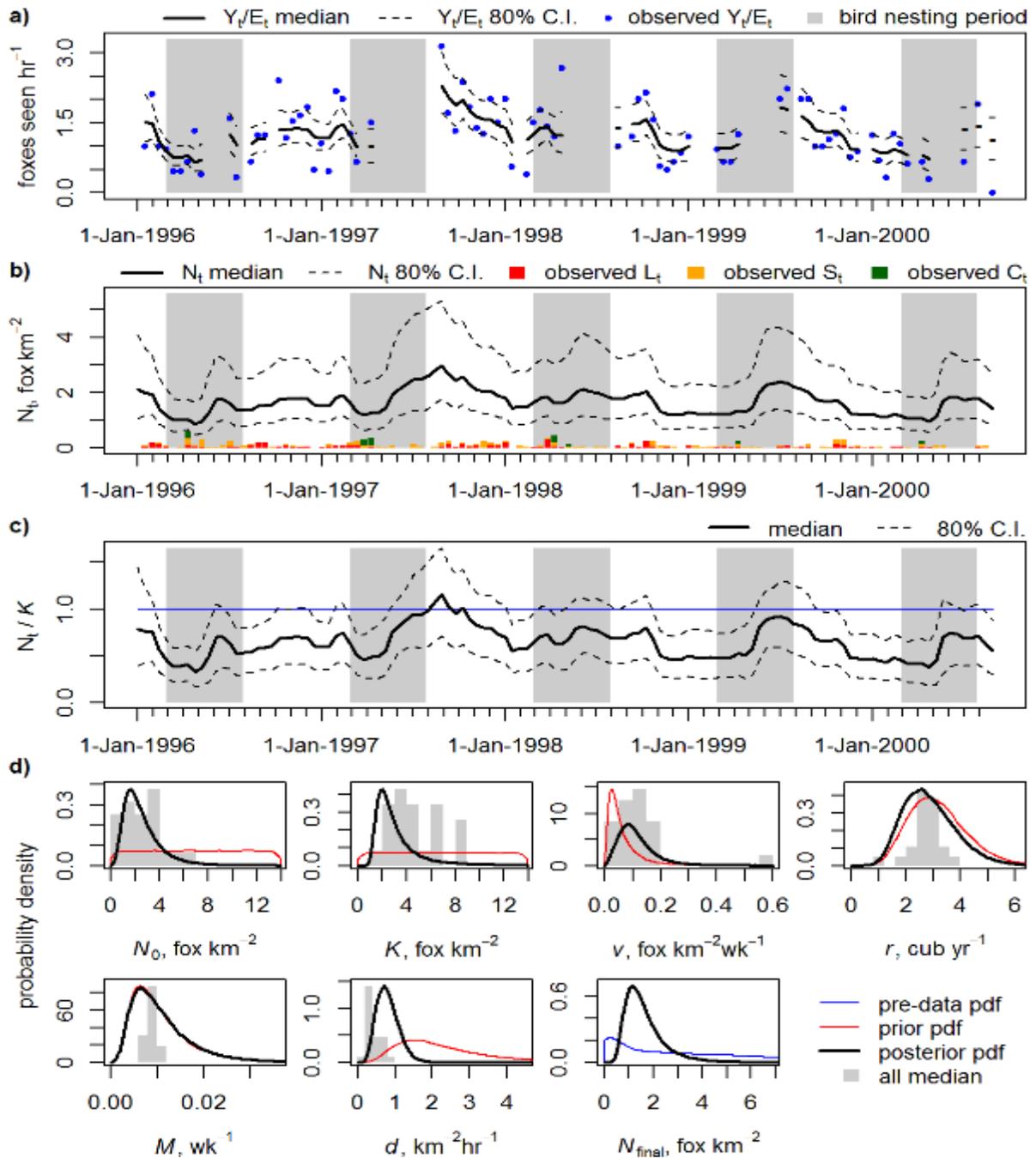


Figure E.8. Results for GDE showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

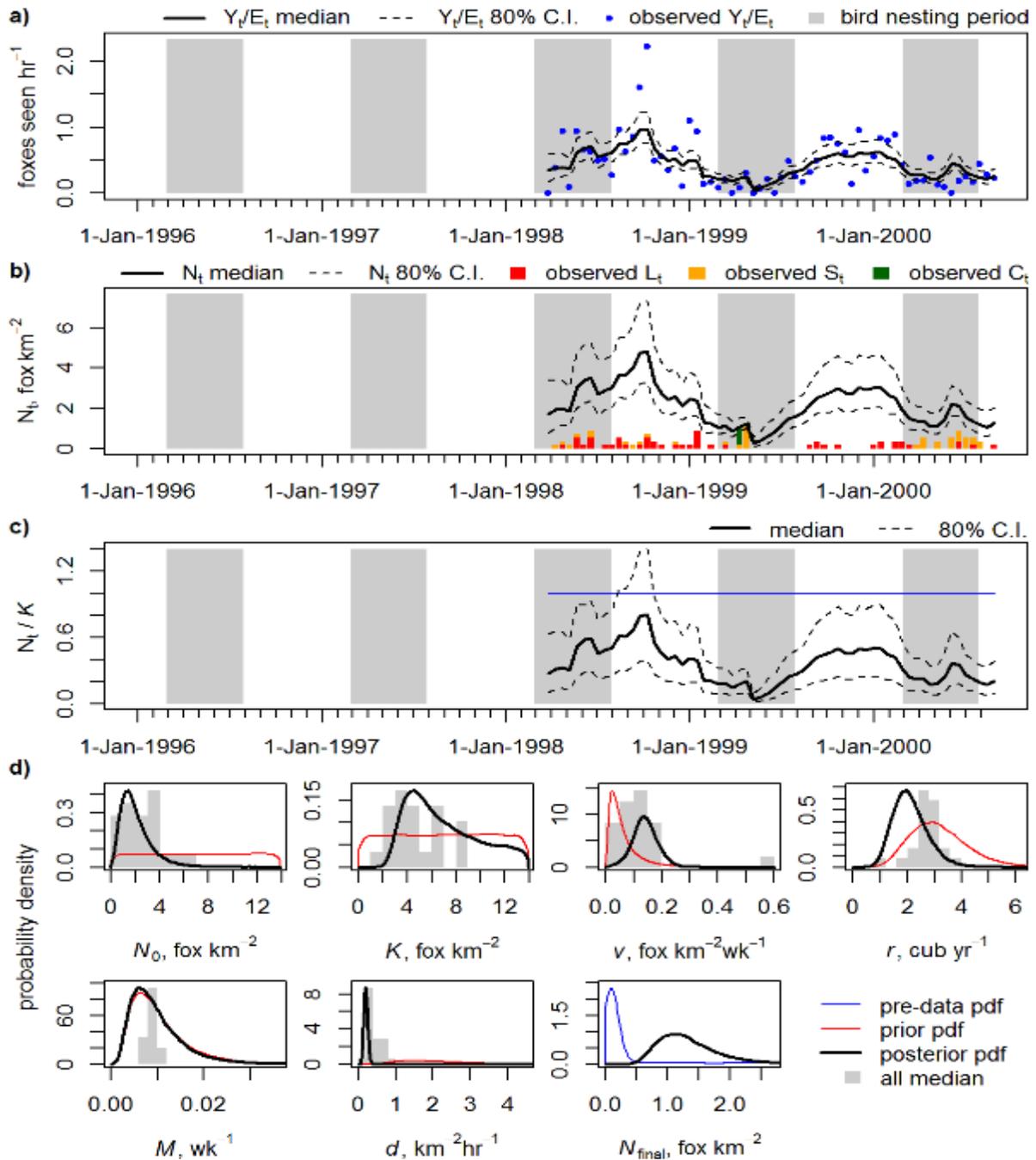


Figure E.9. Results for GHT showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

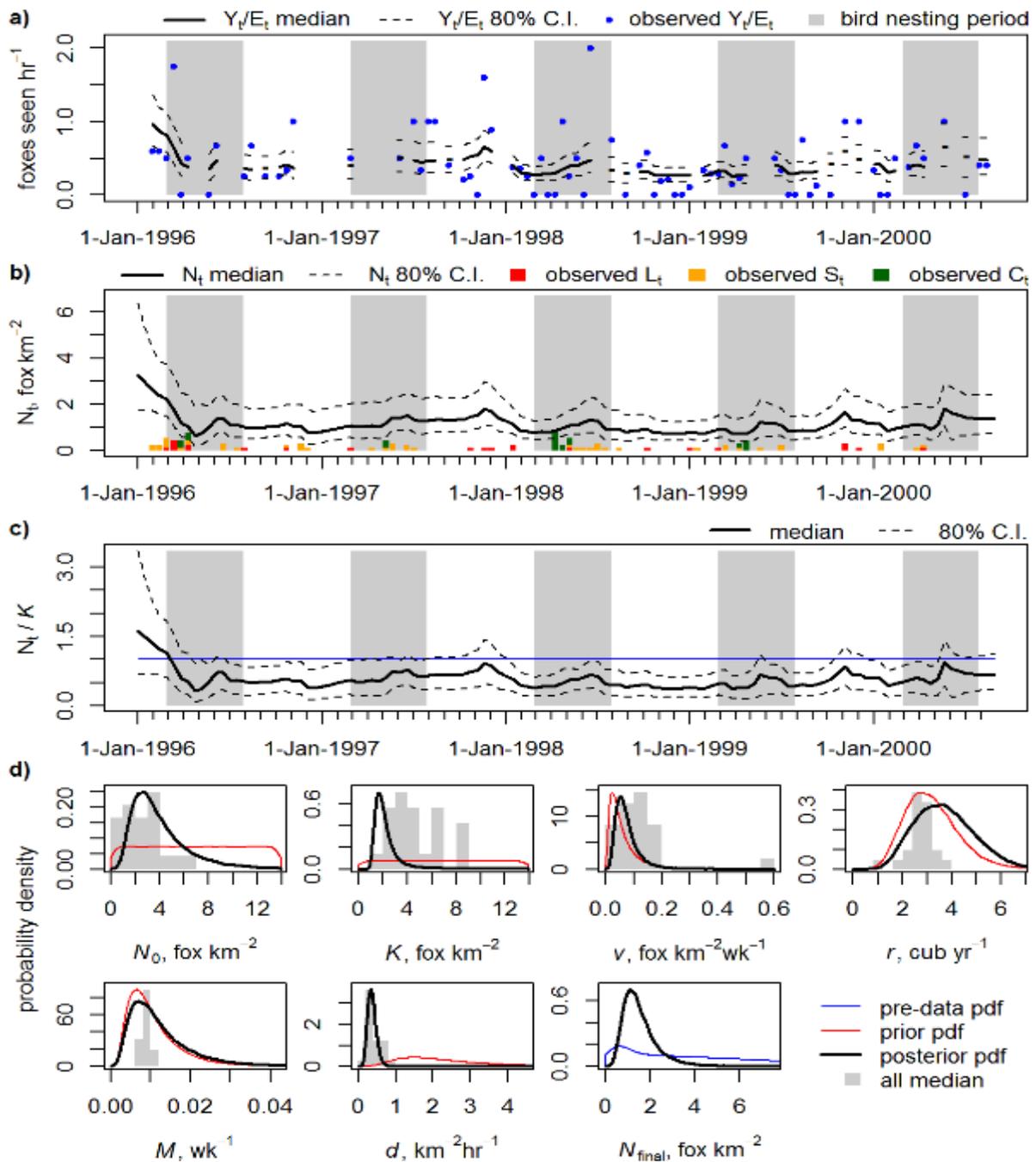


Figure E.10. Results for HUS showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

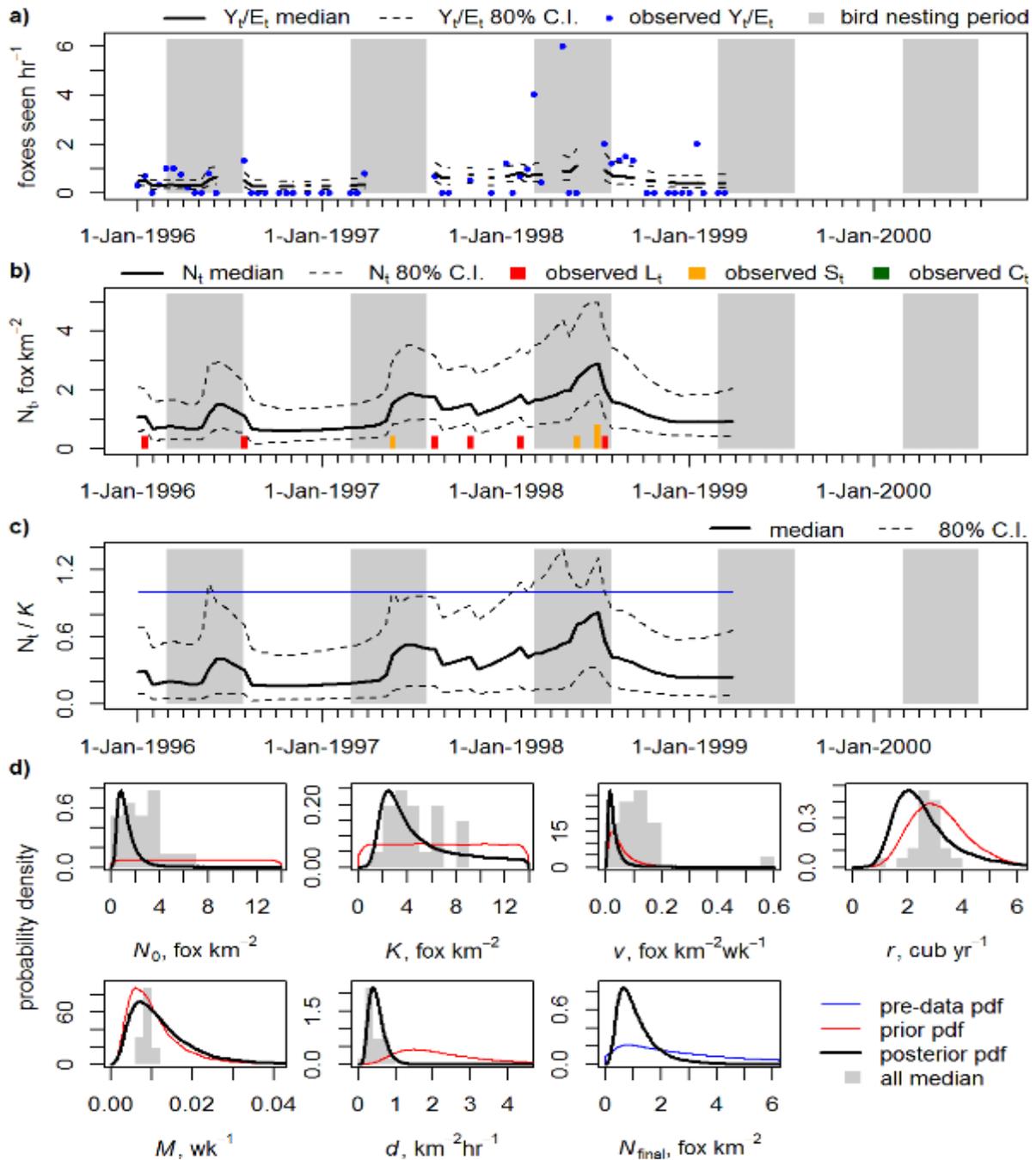


Figure E.11. Results for LEL showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

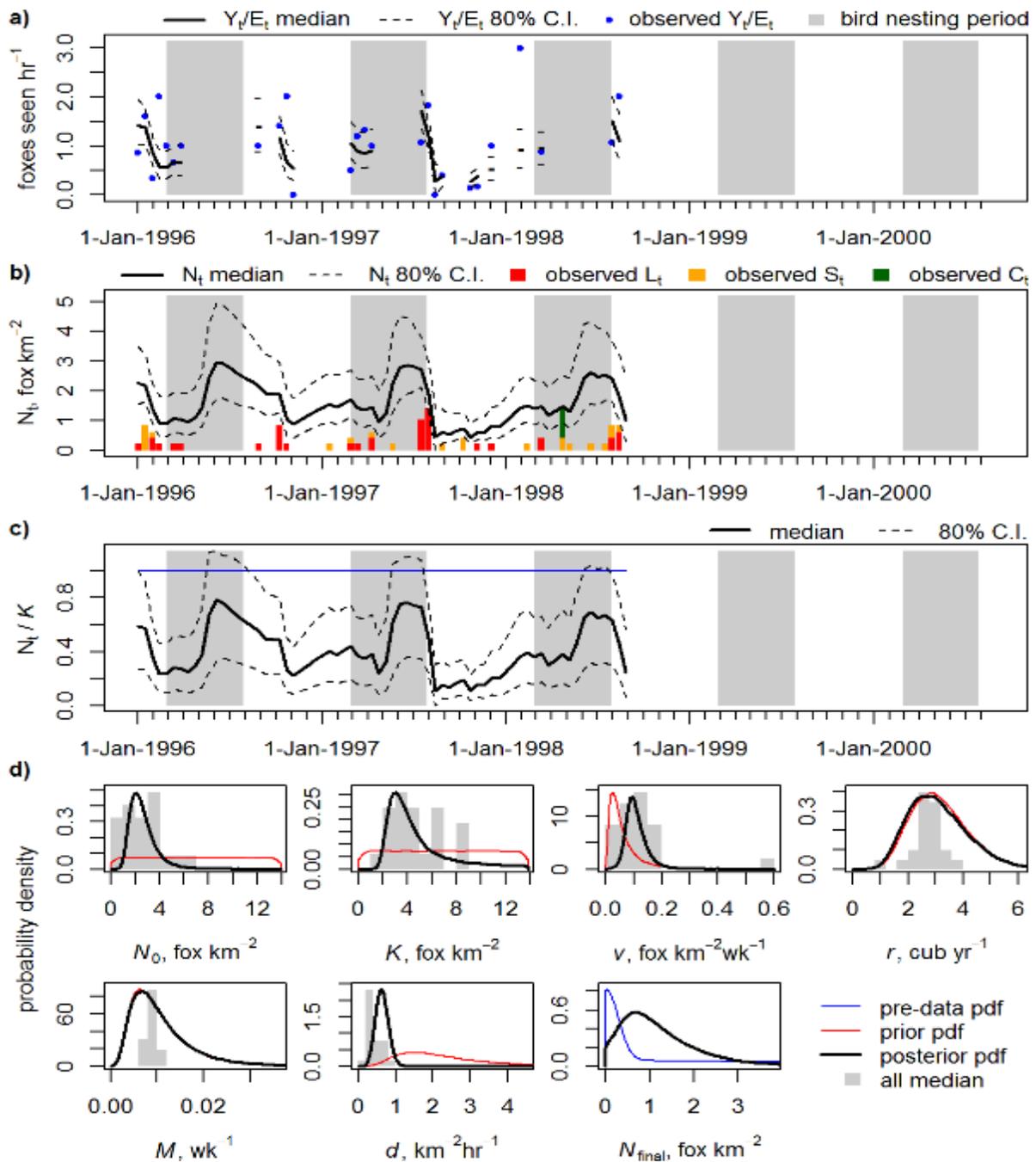


Figure E.12. Results for MAH showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

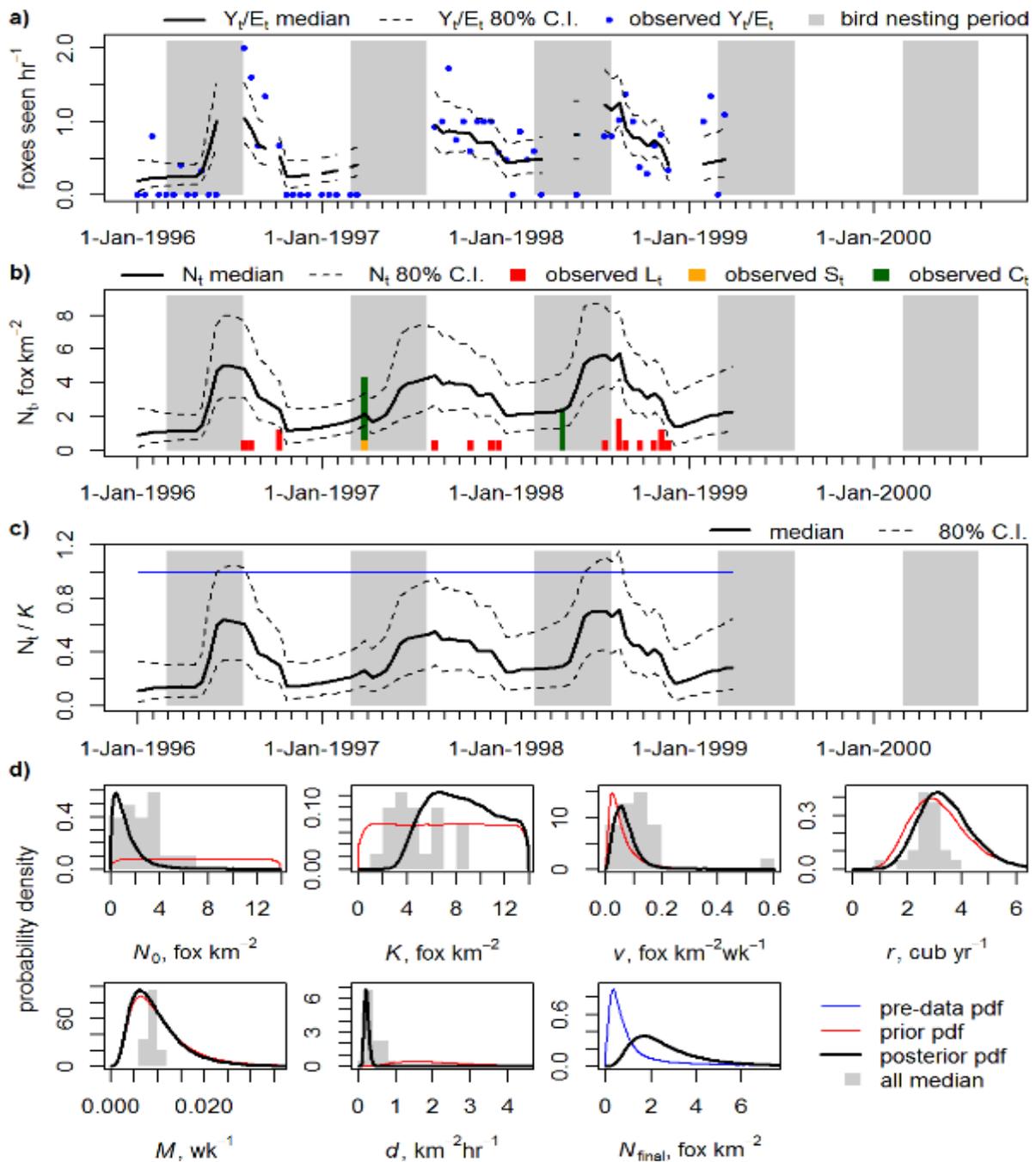


Figure E.13. Results for OCS showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

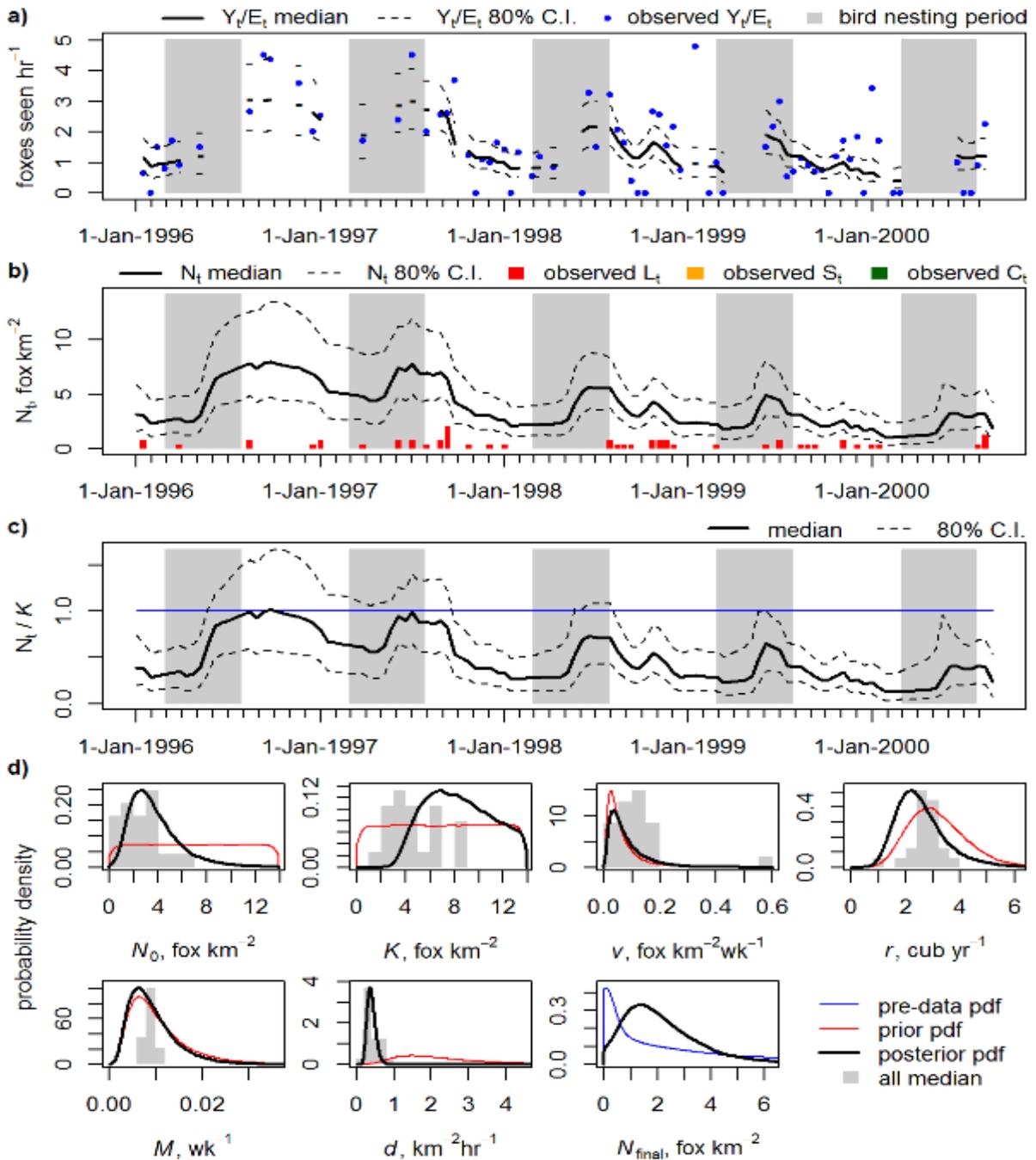


Figure E.14. Results for RAM showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

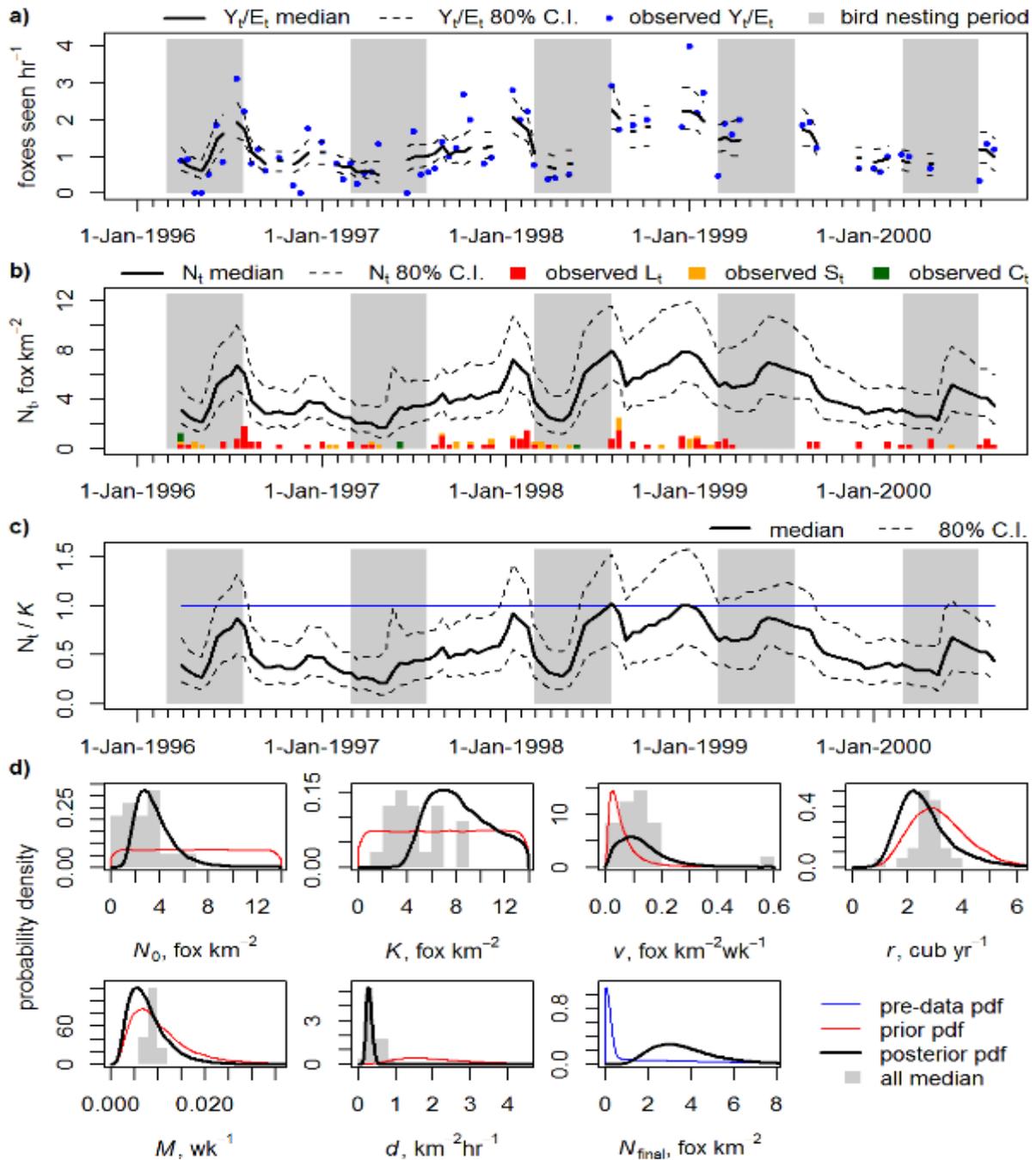


Figure E.15. Results for VDL showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

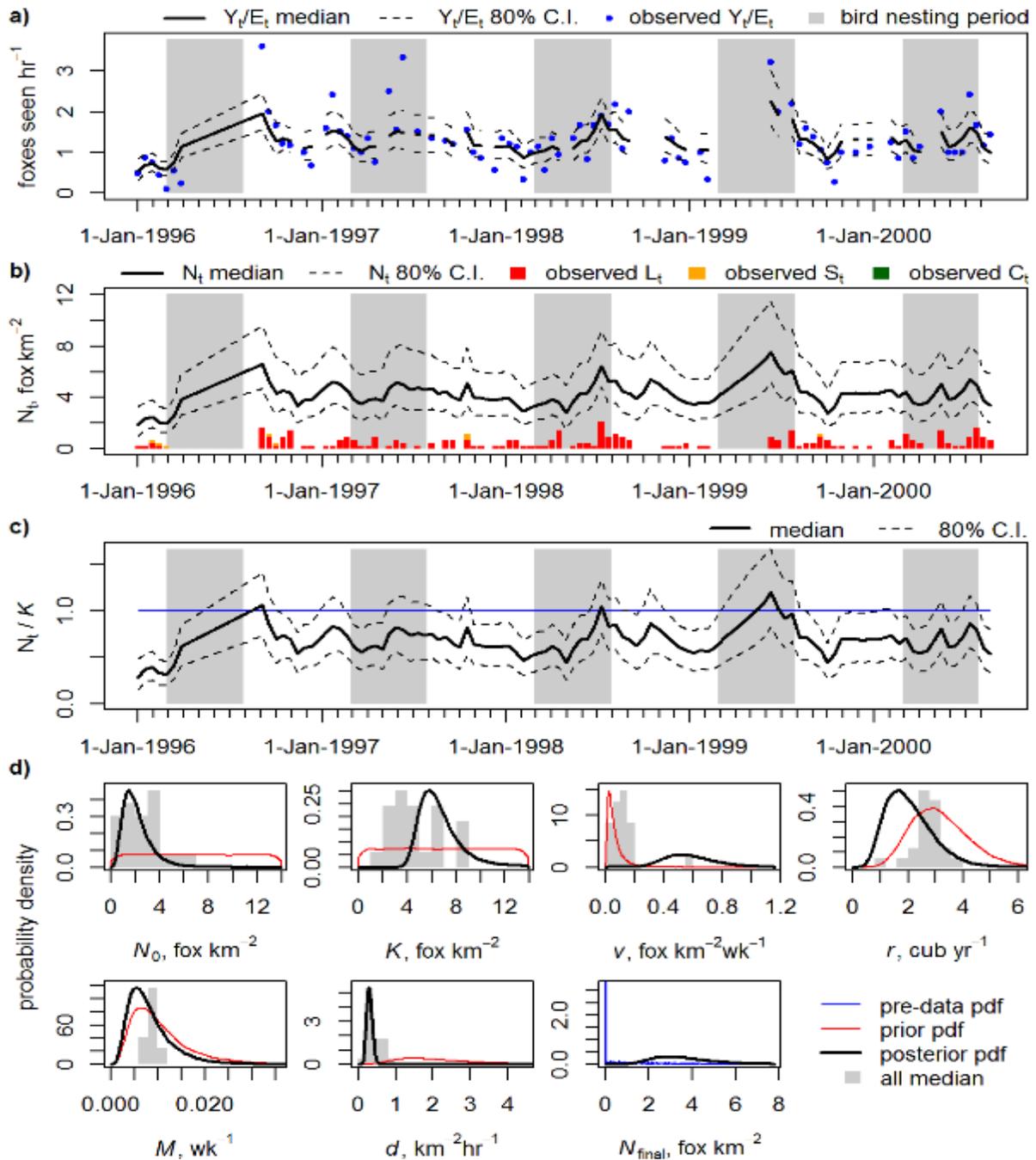


Figure E.16. Results for YEM showing a) posterior fit of the model to sighting rate (Y_t/E_t); b) posterior estimates of bi-weekly fox density (N_t) in relation to the cull removed by different methods; c) estimated N_t as a proportion of carrying capacity (blue line denotes median population at posterior median K); d) priors (or post-model-pre-data distribution) and marginal posteriors of N_0 (initial density), K (carrying capacity), v (immigration rate), r (*per capita* birth rate), M (instantaneous non-culling mortality rate), d (rate of successful search), and fox density in the final time-step. Histograms in panel d) show posterior medians from all estates. In panels a-c) the bird nesting period is shown as a reference.

Appendix F Sensitivity to observation error specification

This Appendix contains the results of the sensitivity analyses that examined the effect on parameter estimates and fox density reconstruction of 1) use of different likelihood functions to model the sightings where σ_p was fixed at 0.2, and 2) use of different likelihood functions to model the sightings where σ_p was estimated using a vague priors. The results support the use of the Poisson distribution to model the sighting data.

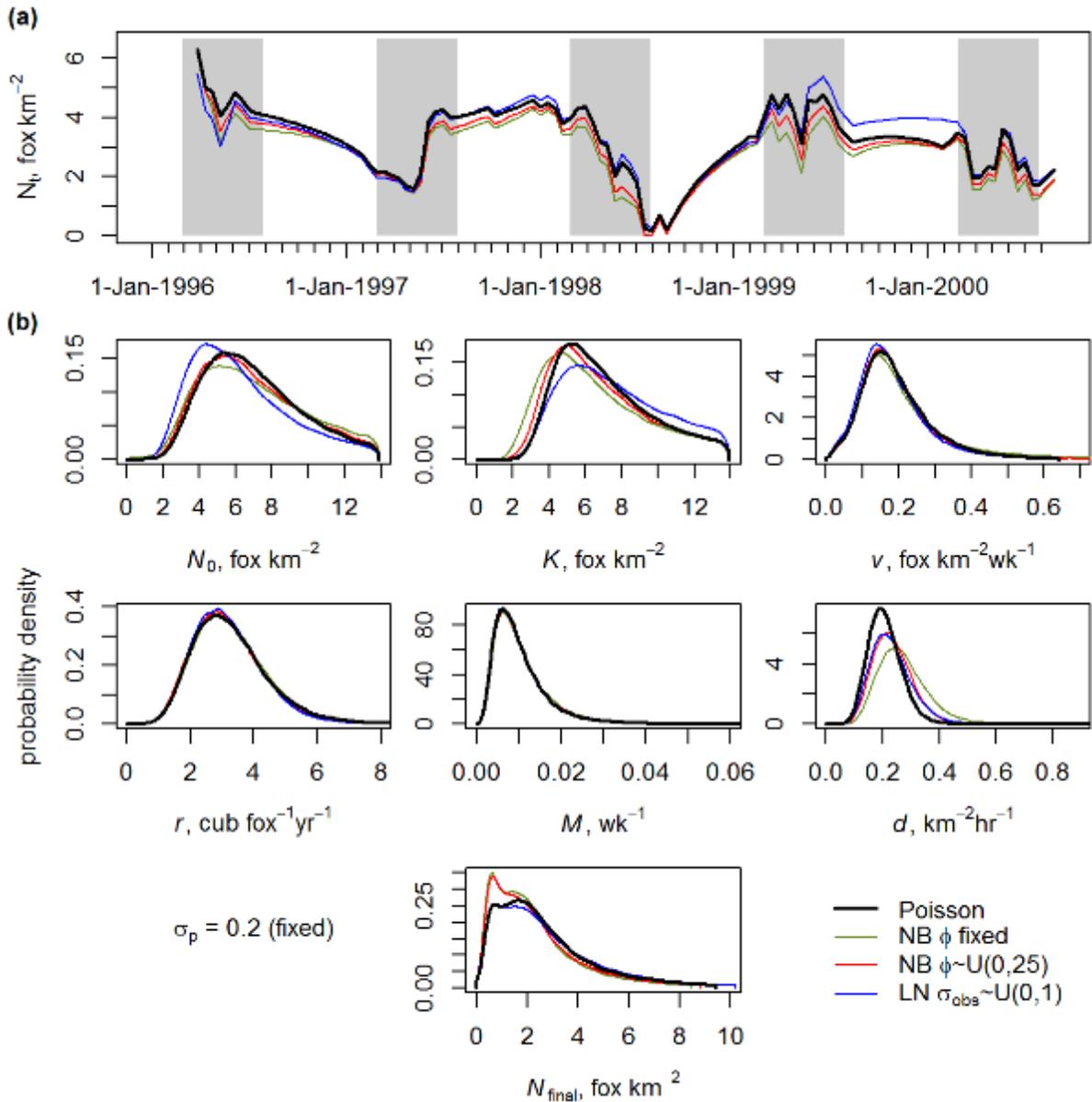


Figure F.1. Results for DLQ showing sensitivity of a) posterior median fox density and b) marginal posterior parameter estimates to specification of the observation error. Process error standard deviation, σ_p , was fixed at 0.2. Observation errors were either assumed to be Poisson, negative binomial (NB), or lognormal (LN). The dispersion parameter, ϕ , of NB errors was either fixed at the maximum likelihood value estimated from the data prior to running of the estimation model or was estimated using a uniform prior with lower and upper bounds of 0 and 25, respectively. The standard deviation, σ_{obs} , in LN errors was estimated using a uniform prior with lower and upper bounds of 0 and 1, respectively. The reference case with Poisson observation errors is shown in bold.

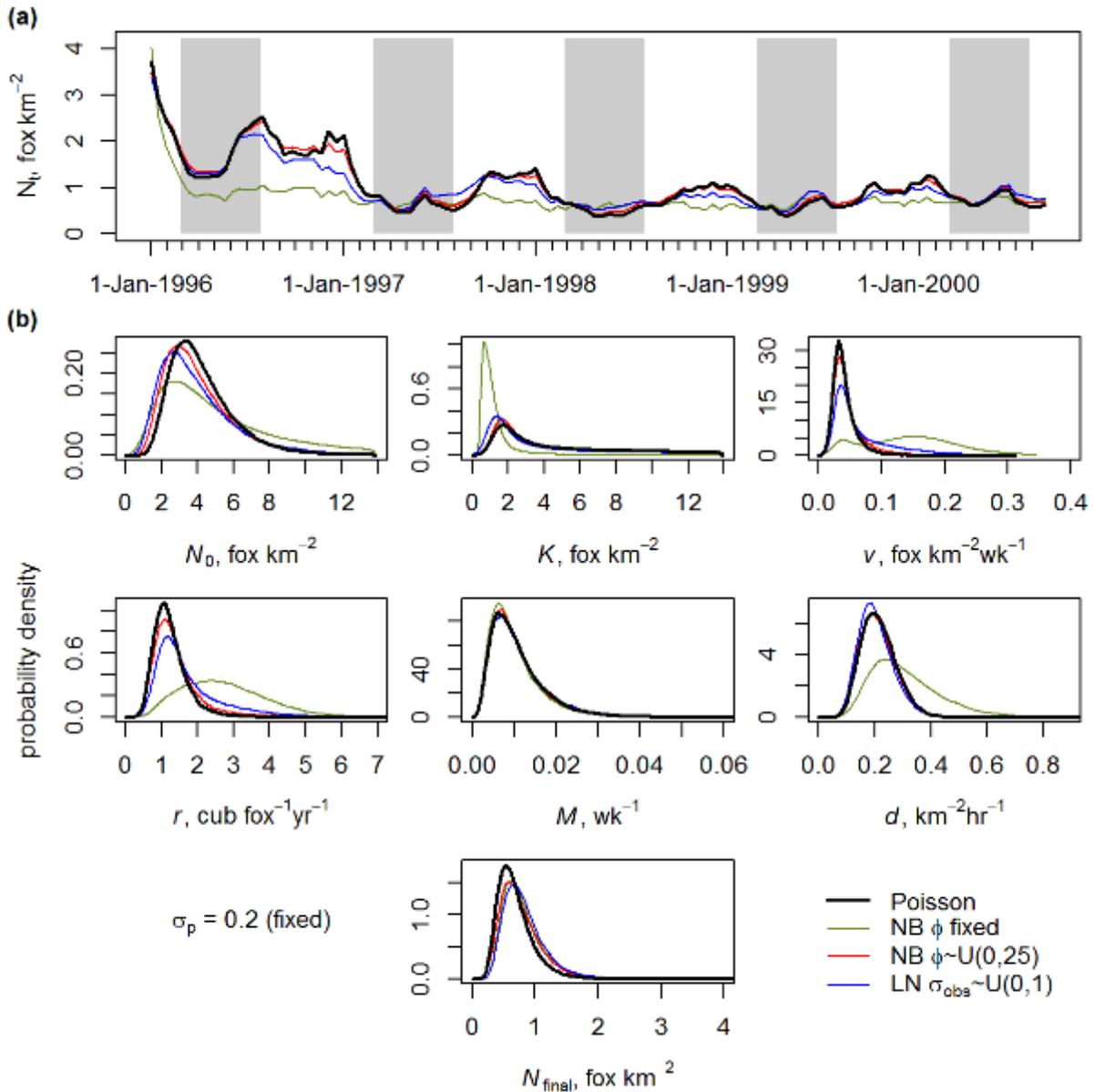


Figure F.2. Results for VAR showing sensitivity of a) posterior median fox density and b) marginal posterior parameter estimates to specification of the observation error. Process error standard deviation, σ_p , was fixed at 0.2. Observation errors were either assumed to be Poisson, negative binomial (NB), or lognormal (LN). The dispersion parameter, ϕ , of NB errors was either fixed at the maximum likelihood value estimated from the data prior to running of the estimation model or was estimated using a uniform prior with lower and upper bounds of 0 and 1, respectively. The standard deviation, σ_{obs} , in LN errors was estimated using a uniform prior with lower and upper bounds of 0 and 1, respectively. The reference case with Poisson observation errors is shown in bold.

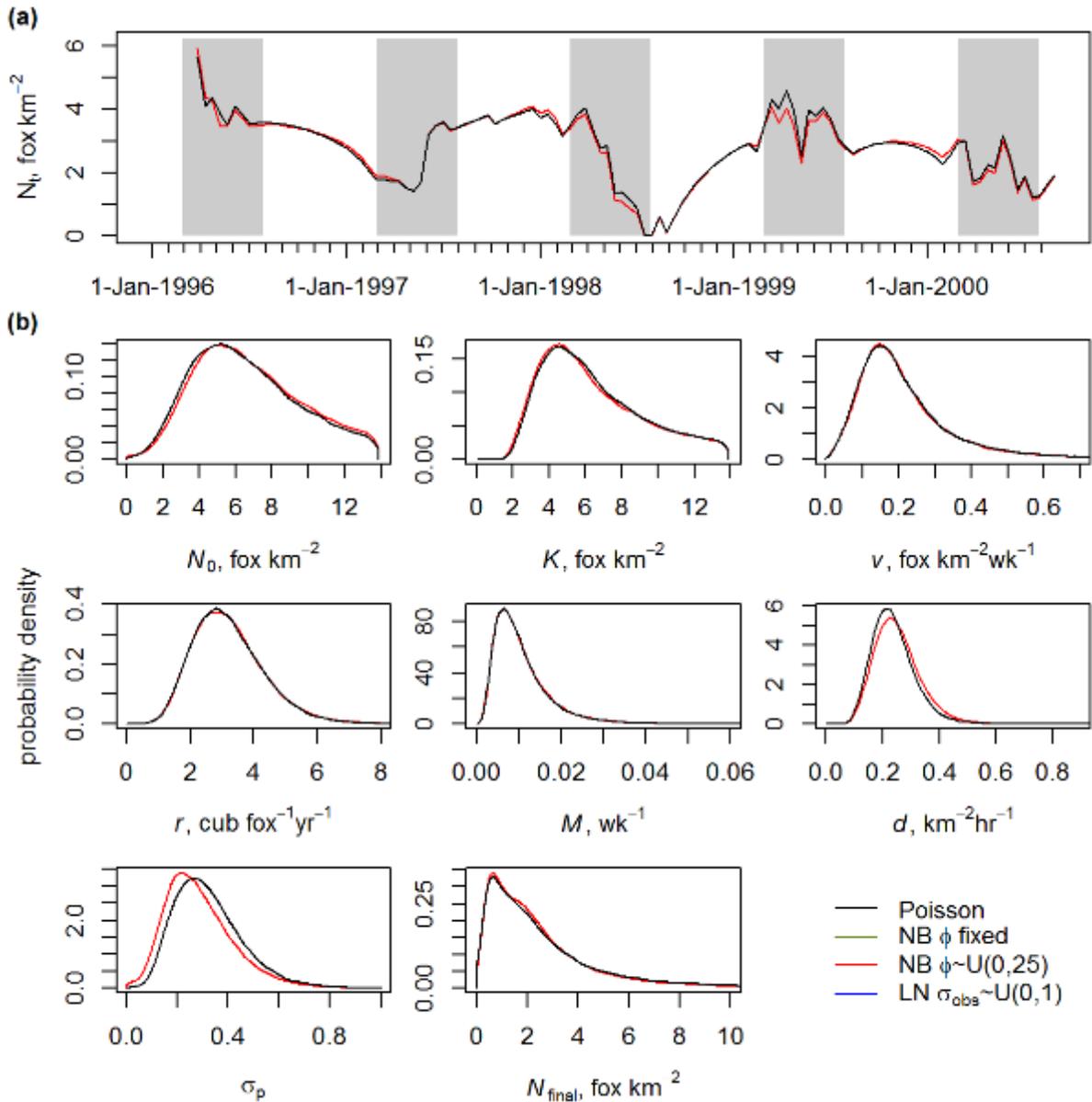


Figure F.3. Results for DLQ showing sensitivity of a) posterior median fox density and b) marginal posterior parameter estimates to specification of the observation error. Process error standard deviation, σ_p , was estimated using a uniform prior with lower and upper bounds of 0.001 and 1.0, respectively. Observation errors were either assumed to be Poisson, negative binomial (NB), or lognormal (LN). The dispersion parameter, ϕ , of NB errors was either fixed at the maximum likelihood value estimated from the data prior to running of the estimation model or was estimated using a uniform prior with lower and upper bounds of 0 and 1, respectively. The standard deviation, σ_{obs} , in LN errors was estimated using a uniform prior with lower and upper bounds of 0 and 1, respectively.

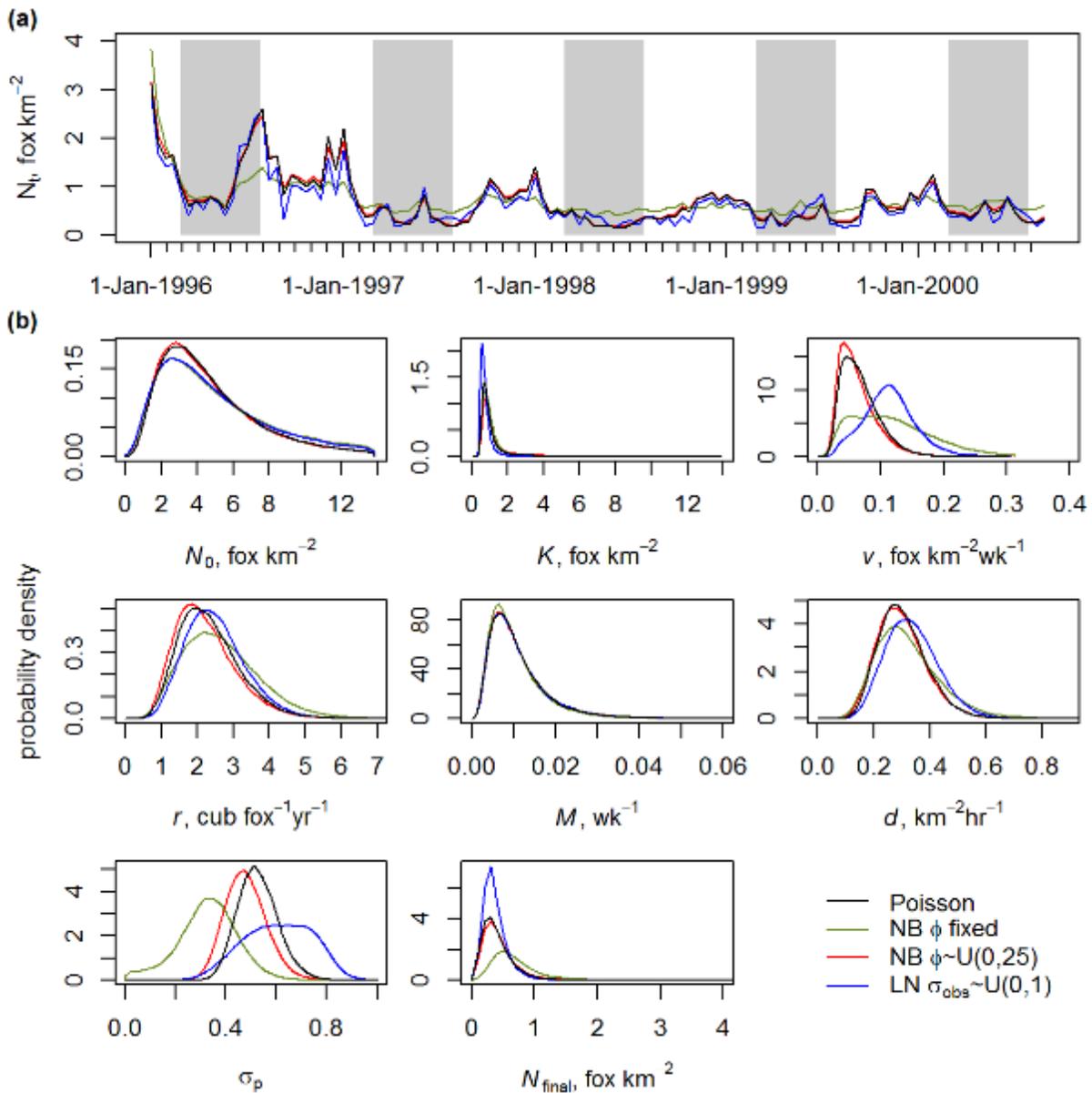


Figure F.4. Results for VAR showing sensitivity of a) posterior median fox density and b) marginal posterior parameter estimates to specification of the observation error. Process error standard deviation, σ_p , was estimated using a uniform prior with lower and upper bounds of 0.001 and 1.0, respectively. Observation errors were either assumed to be Poisson, negative binomial (NB), or lognormal (LN). The dispersion parameter, ϕ , of NB errors was either fixed at the maximum likelihood value estimated from the data prior to running of the estimation model or was estimated using a uniform prior with lower and upper bounds of 0 and 1, respectively. The standard deviation, σ_{obs} , in LN errors was estimated using a uniform prior with lower and upper bounds of 0 and 1, respectively.

Appendix G Estimation of the probability of snaring success

G.1 Introduction

Evaluation of different snaring effort levels required the probability of snare capture per fox p_s to be a function of the number of snares nights available. This was achieved by assuming that p_s increased with the number of snare nights following a cumulative geometric distribution function, where probability of success was equal to the daily probability of fox capture per snare f . An estimate of f was obtained using time-to-event analysis of detailed data on fox capture histories of individual snare locations.

Survival functions give the probability that an event of interest has not occurred by a given time t . Survival functions such as the Kaplan-Meier (KM) survival curve are non-parametric maximum likelihood estimates of survival over time (Kaplan & Meier 1958). For this example, the event of interest is the fate of a snare location each day which either ‘survives’ to remain operational the following day or ‘terminates’ for some reason, e.g. fox capture or removal without capture. In contrast, cumulative incidence functions (CIFs) give the probability of the event having occurred by time t and can be calculated as the complement of the survival curve, i.e. $\text{CIF} = 1 - \text{KM}$ (Bischof *et al.* 2014). Using this approach, the probability of snare termination following fox capture by time t can be determined empirically.

An alternative approach to calculating a CIF for snares is to use a value for the daily probability of fox capture per snare. Assuming constant fox capture probability over time, the probability P of snare termination by day t after it is set as the result of a fox capture is given by:

$$P(t) = 1 - (1 - f)^t \tag{Eq. G.1}$$

where f is the daily probability of fox capture per snare. This parametric approach has been used elsewhere to construct cumulative incidence function or detectability curves from daily probability of species detection using camera traps (Bischof *et al.* 2014), floral surveys (Garrard *et al.* 2008), or mink rafts (Reynolds *et al.* 2010a). An estimate of f can therefore be

obtained from detailed snare data by fitting a parametric CIF to an empirical CIF calculated as the complement of a Kaplan-Meier survival curve.

G.2 Methods

The FMS data were not suitable for use in this analysis as there was no information on snaring effort. Instead, data from an earlier GWCT study of snaring practices were used. In this dataset (GWCT, unpublished data), 64 gamekeepers operating on estates across Britain made daily records for a total of 1,890 individual snare placements made between August 1993 and August 1995, resulting in the capture of 285 foxes (Figure G.1). Thus the cause of termination and time to termination were known for each snare set. Where snare locations were re-used after the first capture, only the first time-to-capture was considered.

All analysis was performed within the R statistical software (R Core Team 2013). A Kaplan-Meier survival function was fitted to the snare time-to-termination for fox capture data using the ‘survfit’ function within the R survival package (Therneau 2014). The empirical CIF for daily snare termination for fox capture was calculated as the complement to the KM curve. The parametric CIF was calculated using Eq. G.1. The maximum likelihood value for f was estimated by fitting the parametric CIF to the empirical CIF using least-squares. This analysis was repeated using the snare time-to-termination data from all causes to obtain the daily probability of snare termination from all causes.

G.3 Results

The maximum length of time before termination of an individual snare was 428 days. Only 19 snares were set for longer than 365 days and by this time the probability of snare termination from all causes was >0.99 (Figure G.2). The mean number of days before a snare was terminated was 62 days. For a snare that successfully caught a fox, the mean number of days before capture was 47 days. 50% of all snares set have caught a fox or been terminated for some other reason by 42 days. The probability that a snare would be terminated by a fox capture by day 365 was 0.396 (Figure G.2, Figure G.3).

From the fit to the empirical CIFs, the daily probability of snare termination from all causes was estimated to be 0.0167, and the daily probability of fox capture per snare was 0.00175 (Figure G.3). It is important to comment on the fit of the parametric CIF to the empirical CIF for fox captures, as the poor fit was caused by the need to account for snare termination from all snares operating and not just those snares that caught foxes. A closer fit to the empirical CIF can be achieved by multiplying the right-hand side of Eq. G. by the expected proportion of all snares terminating from fox capture after 365 days (0.396), and then re-fitting the equation. However, the estimated value (0.00807) is then an overestimate of the daily probability of fox capture per snare as it is only considering snares which were successful. Until capture this is obviously unknown. Therefore the value of f used to determine the probability of snare capture per fox was 0.00175. It must be noted that this estimate of f represents a mean daily probability of fox capture given the fox densities on the estates the contributing gamekeepers were operating on.

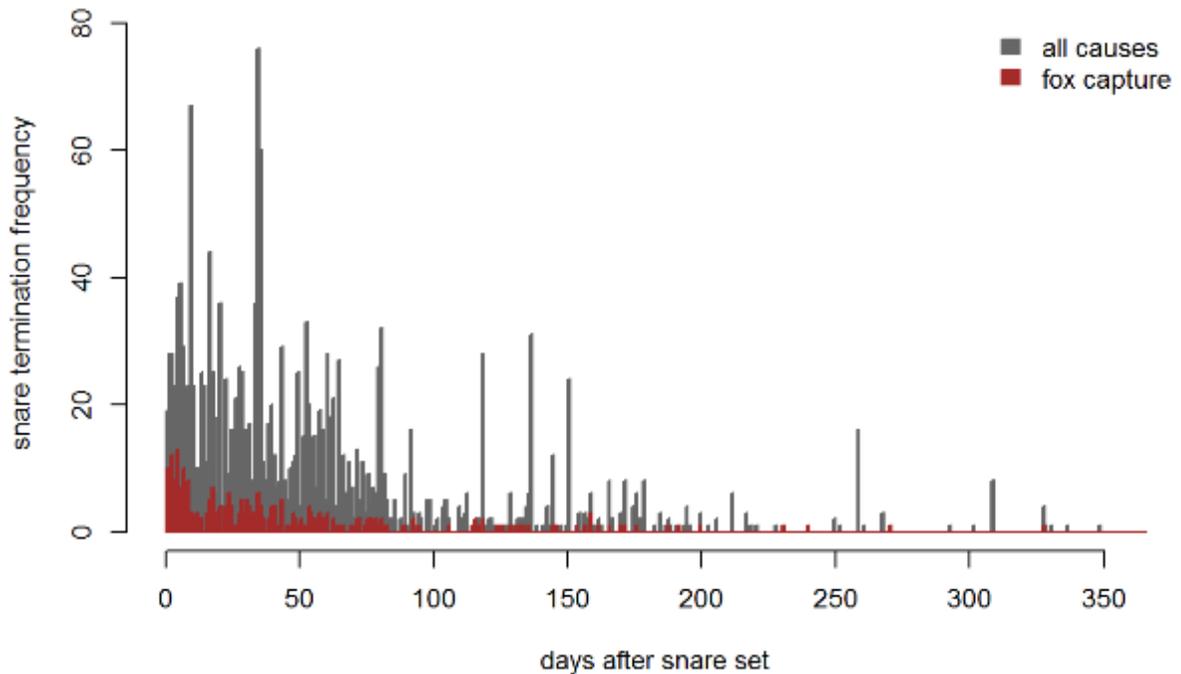


Figure G.1. Data from individual snare locations showing the time-to-termination from all causes and the time-to-termination from fox captures only.

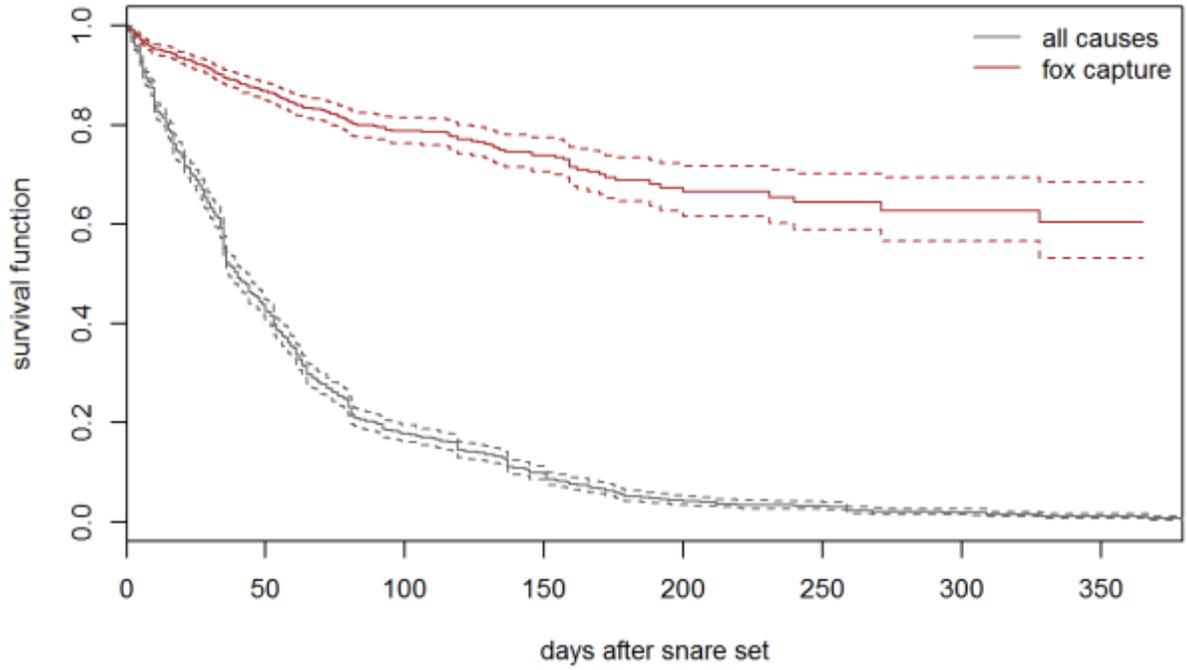


Figure G.2. Kaplan-Meier survival function showing the cumulative probability that a snare will not have been terminated due to any cause (grey) or due to fox capture (brown). Dashed lines indicate the 95% confidence limits.

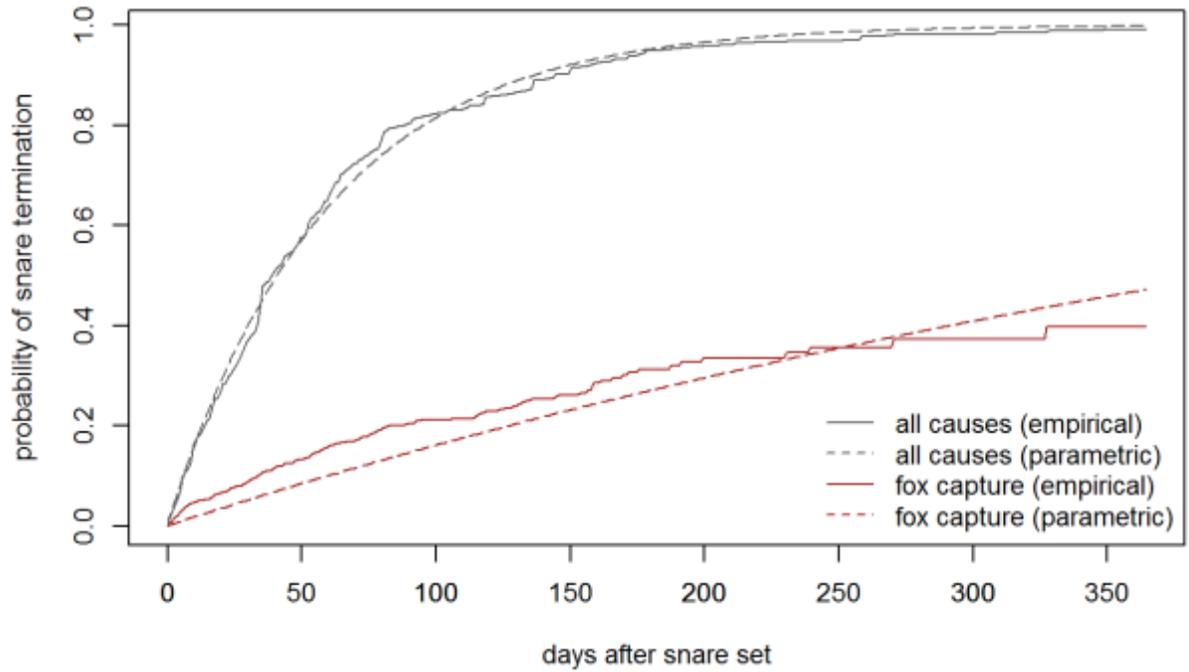


Figure G.3. Cumulative incidence functions showing time-to-termination of snares from all causes (grey) and from fox captures (brown). Solid lines are empirical CIFs obtained as the complement of Kaplan-Meier survival functions. Dashed lines are best-fit parametric CIFs based upon the daily probability of fox capture per snare f .

Appendix H Open-loop scatterplots for other estates

This Appendix shows the open-loop results from estates not shown in Chapter 8.

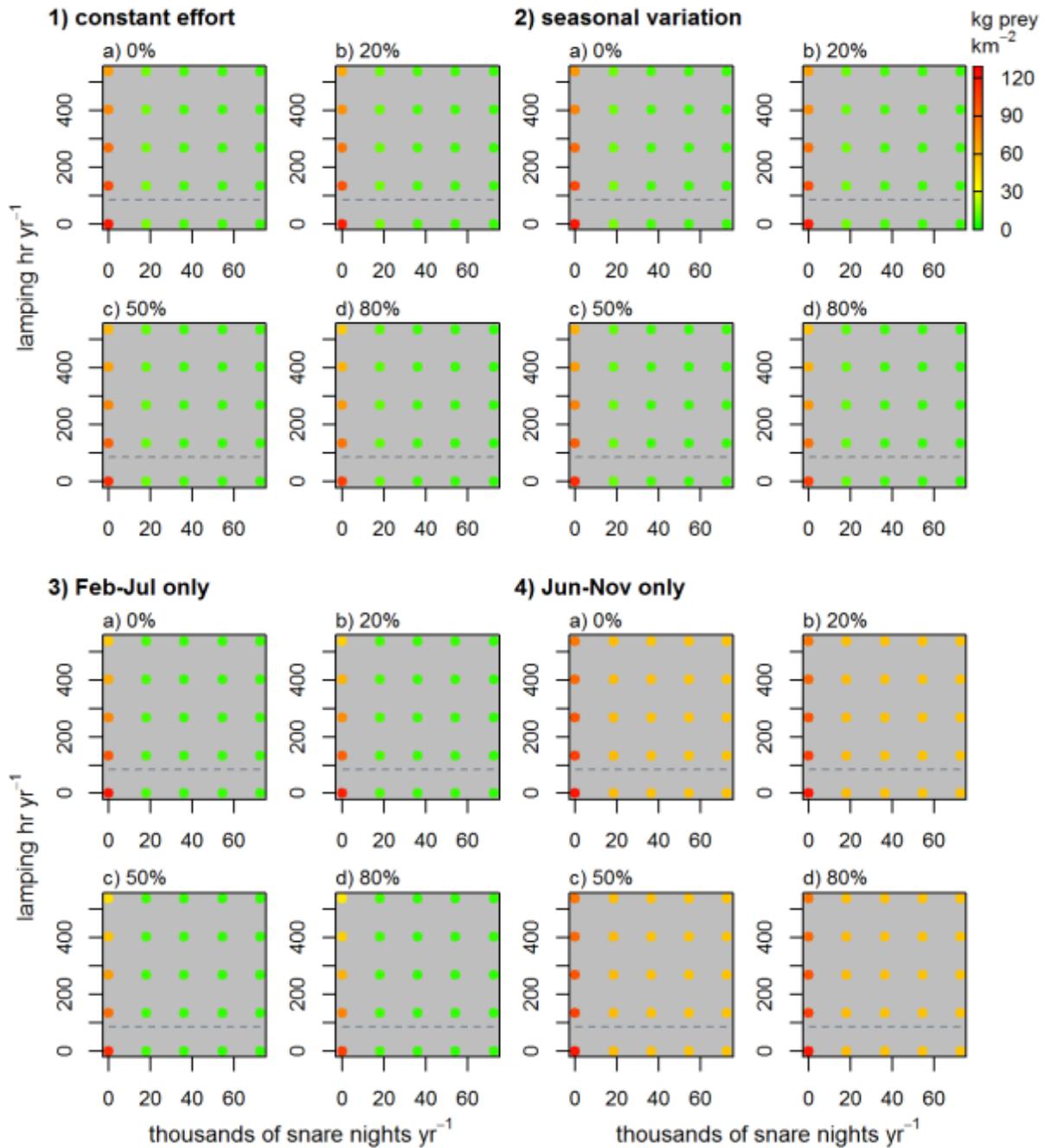


Figure H.1. Scatterplots showing results of open-loop management strategy evaluation for GDE under different levels of culling effort. Colour scale ranges from high food requirements (red) to low food requirements (green). Figures are arranged in sets of four by strategy 1) year-round uniform, 2) year-round with seasonal lamping variation, 3) spring (Feb-Jul) control only, and 4) autumn (Jun-Nov) control only. Figures a)-d) within each strategy set refer to different percentages of cubs killed at earths. Dashed horizontal lines show the mean observed level of lamping effort on this estate.

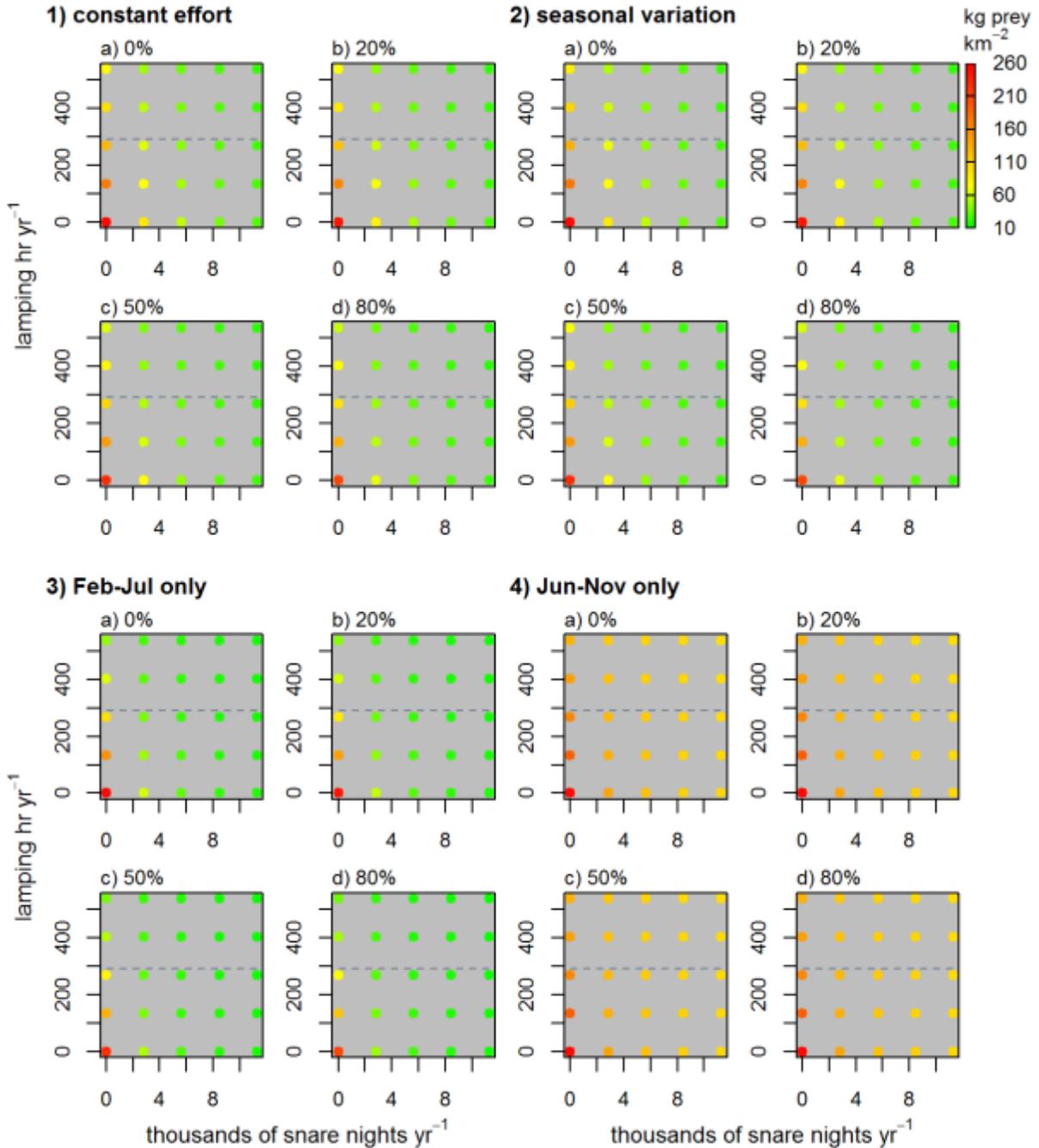


Figure H.2. Scatterplots showing results of open-loop management strategy evaluation for GHT under different levels of culling effort. Colour scale ranges from high food requirements (red) to low food requirements (green). Figures are arranged in sets of four by strategy 1) year-round uniform, 2) year-round with seasonal lamping variation, 3) spring (Feb-Jul) control only, and 4) autumn (Jun-Nov) control only. Figures a)-d) within each strategy set refer to different percentages of cubs killed at earths. Dashed horizontal lines show the mean observed level of lamping effort on this estate.

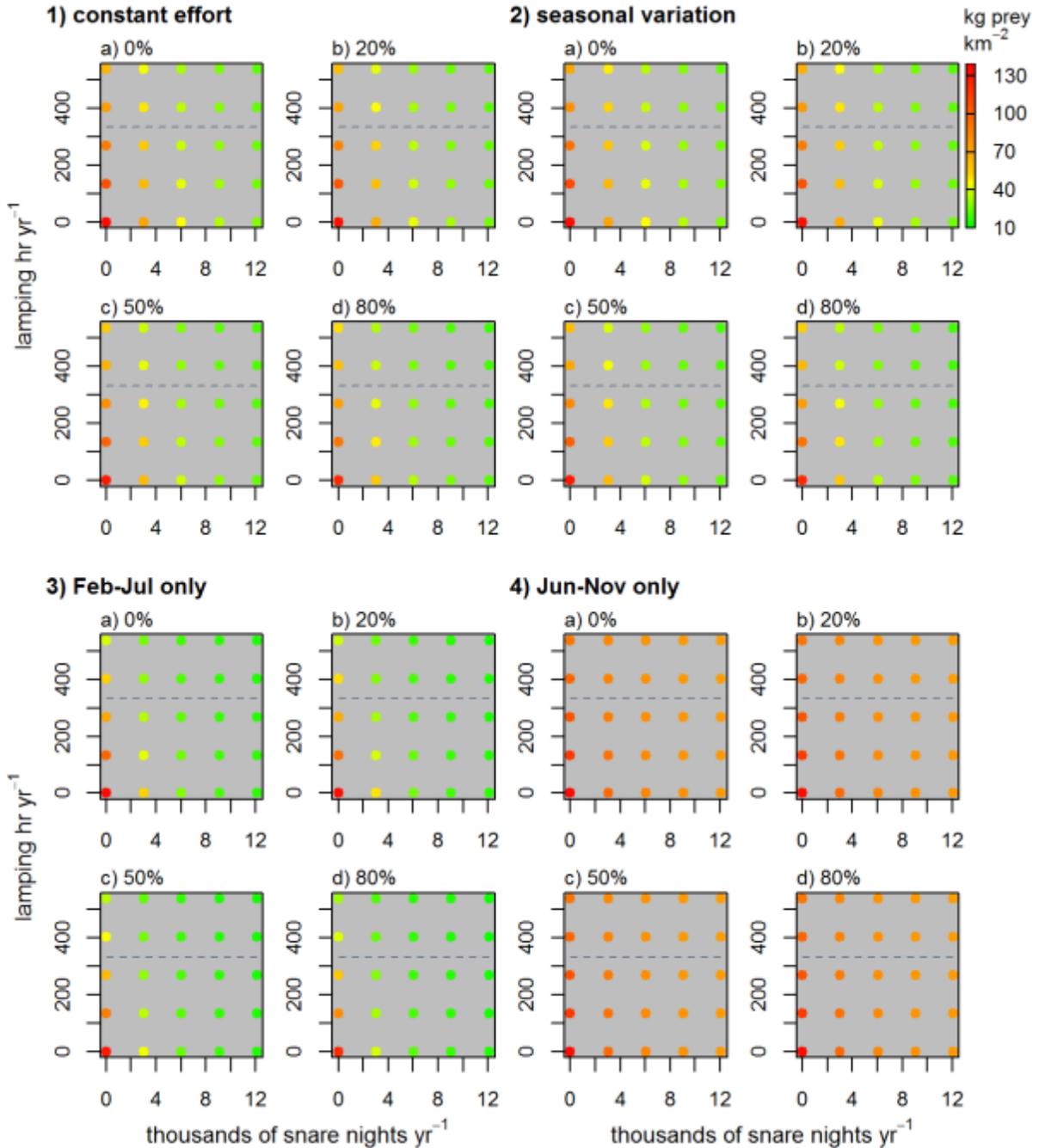


Figure H.3. Scatterplots showing results of open-loop management strategy evaluation for HIR under different levels of culling effort. Colour scale ranges from high food requirements (red) to low food requirements (green). Figures are arranged in sets of four by strategy 1) year-round uniform, 2) year-round with seasonal lamping variation, 3) spring (Feb-Jul) control only, and 4) autumn (Jun-Nov) control only. Figures a)-d) within each strategy set refer to different percentages of cubs killed at earths. Dashed horizontal lines show the mean observed level of lamping effort on this estate.

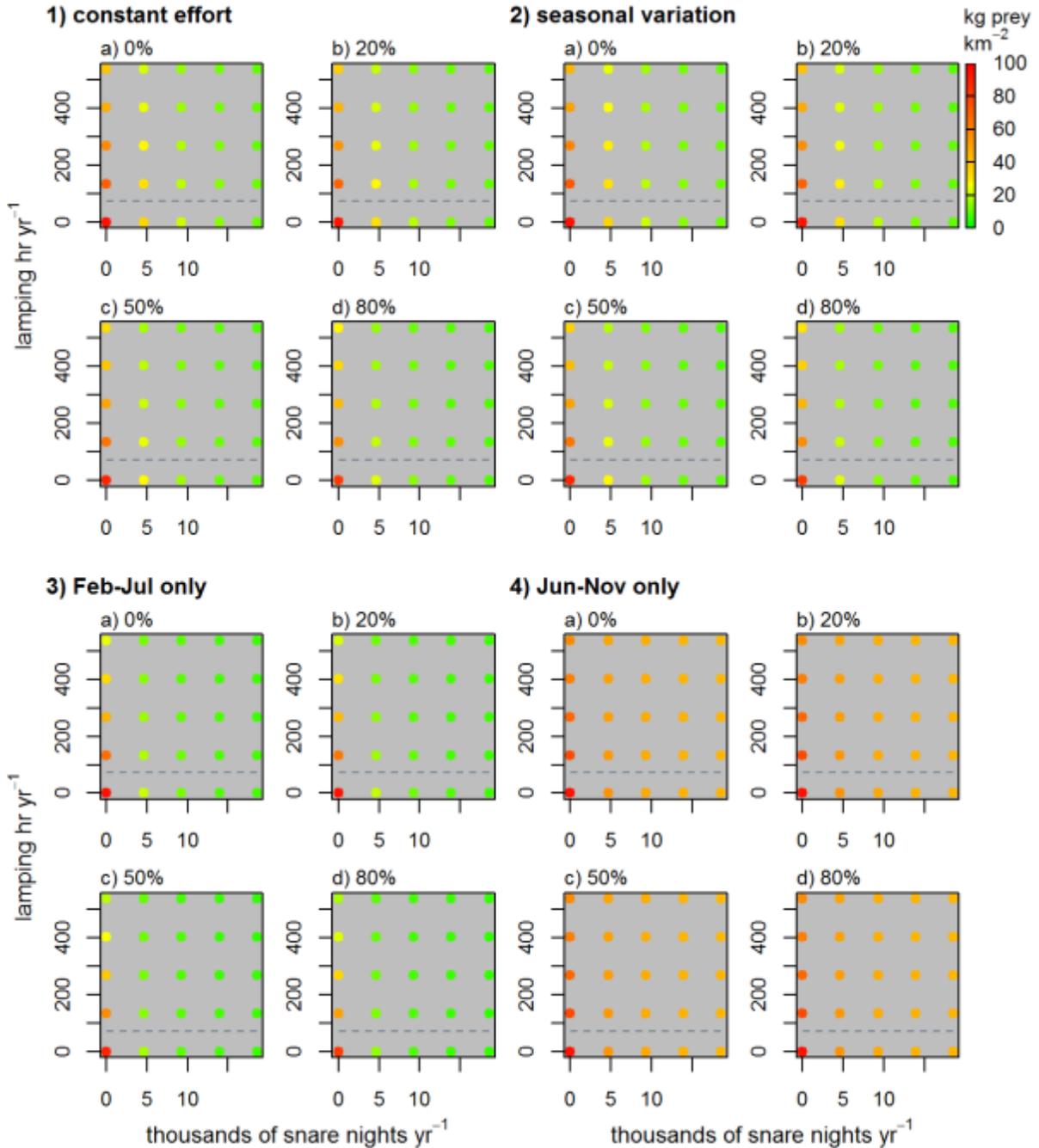


Figure H.4. Scatterplots showing results of open-loop management strategy evaluation for HUS under different levels of culling effort. Colour scale ranges from high food requirements (red) to low food requirements (green). Figures are arranged in sets of four by strategy 1) year-round uniform, 2) year-round with seasonal lamping variation, 3) spring (Feb-Jul) control only, and 4) autumn (Jun-Nov) control only. Figures a)-d) within each strategy set refer to different percentages of cubs killed at earths. Dashed horizontal lines show the mean observed level of lamping effort on this estate.

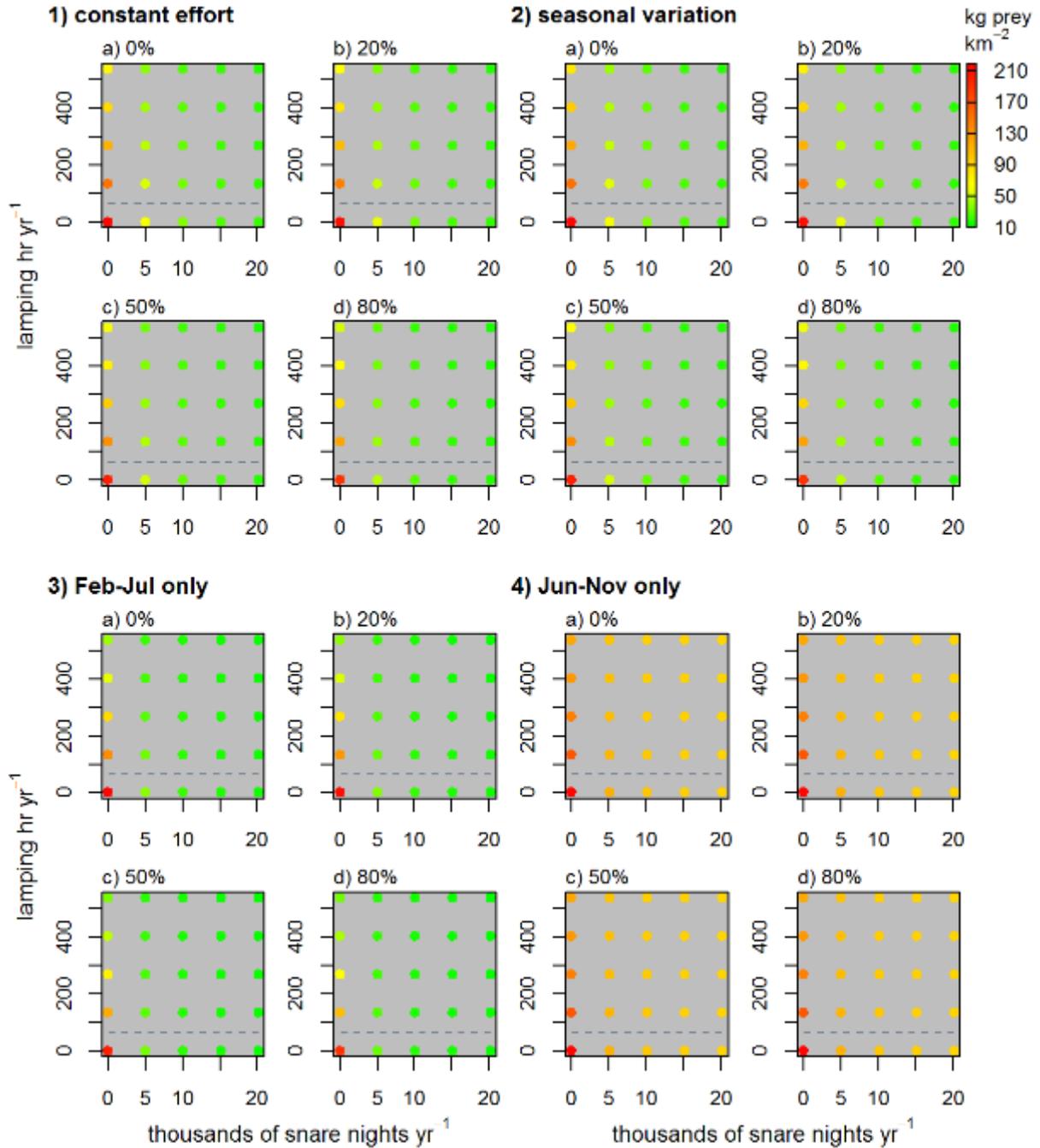


Figure H.5. Scatterplots showing results of open-loop management strategy evaluation for NYP under different levels of culling effort. Colour scale ranges from high food requirements (red) to low food requirements (green). Figures are arranged in sets of four by strategy 1) year-round uniform, 2) year-round with seasonal lamping variation, 3) spring (Feb-Jul) control only, and 4) autumn (Jun-Nov) control only. Figures a)-d) within each strategy set refer to different percentages of cubs killed at earths. Dashed horizontal lines show the mean observed level of lamping effort on this estate.

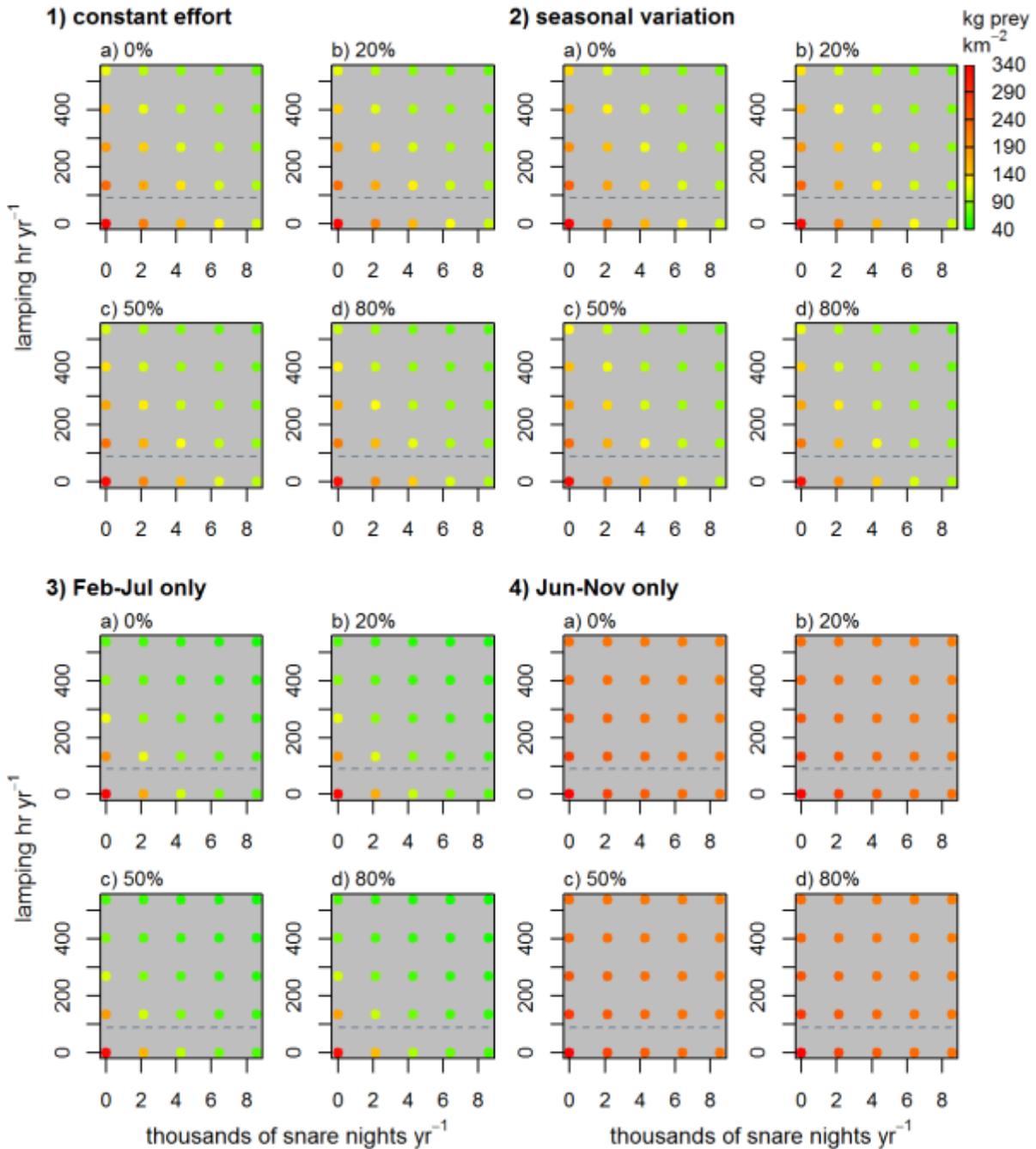


Figure H.6. Scatterplots showing results of open-loop management strategy evaluation for YEM under different levels of culling effort. Colour scale ranges from high food requirements (red) to low food requirements (green). Figures are arranged in sets of four by strategy 1) year-round uniform, 2) year-round with seasonal lamping variation, 3) spring (Feb-Jul) control only, and 4) autumn (Jun-Nov) control only. Figures a)-d) within each strategy set refer to different percentages of cubs killed at earths. Dashed horizontal lines show the mean observed level of lamping effort on this estate.

Appendix I Effect of method on other estates

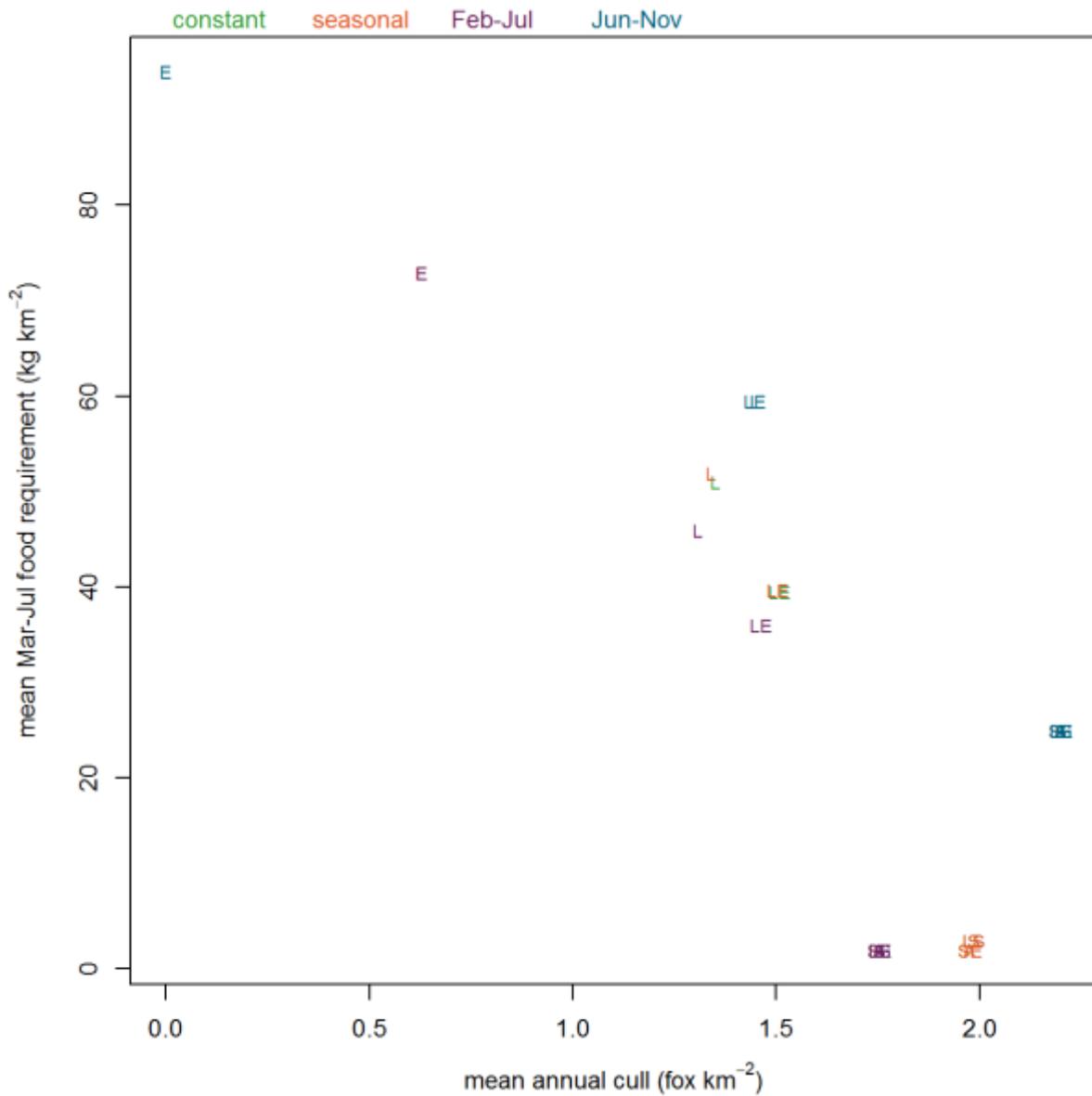


Figure I.1. Trade-offs between the effectiveness of different combinations of culling methods at reducing the food requirement during the nesting period and the number of foxes which must be killed annually to achieve this level of control on the VAR estate. Letters refer to each culling method (or combination thereof): L = lamping, S = snaring, E = cubs killed at earths, A = all methods. Results are from open-loop MSE and are shown under the maximum levels of effort for each method.

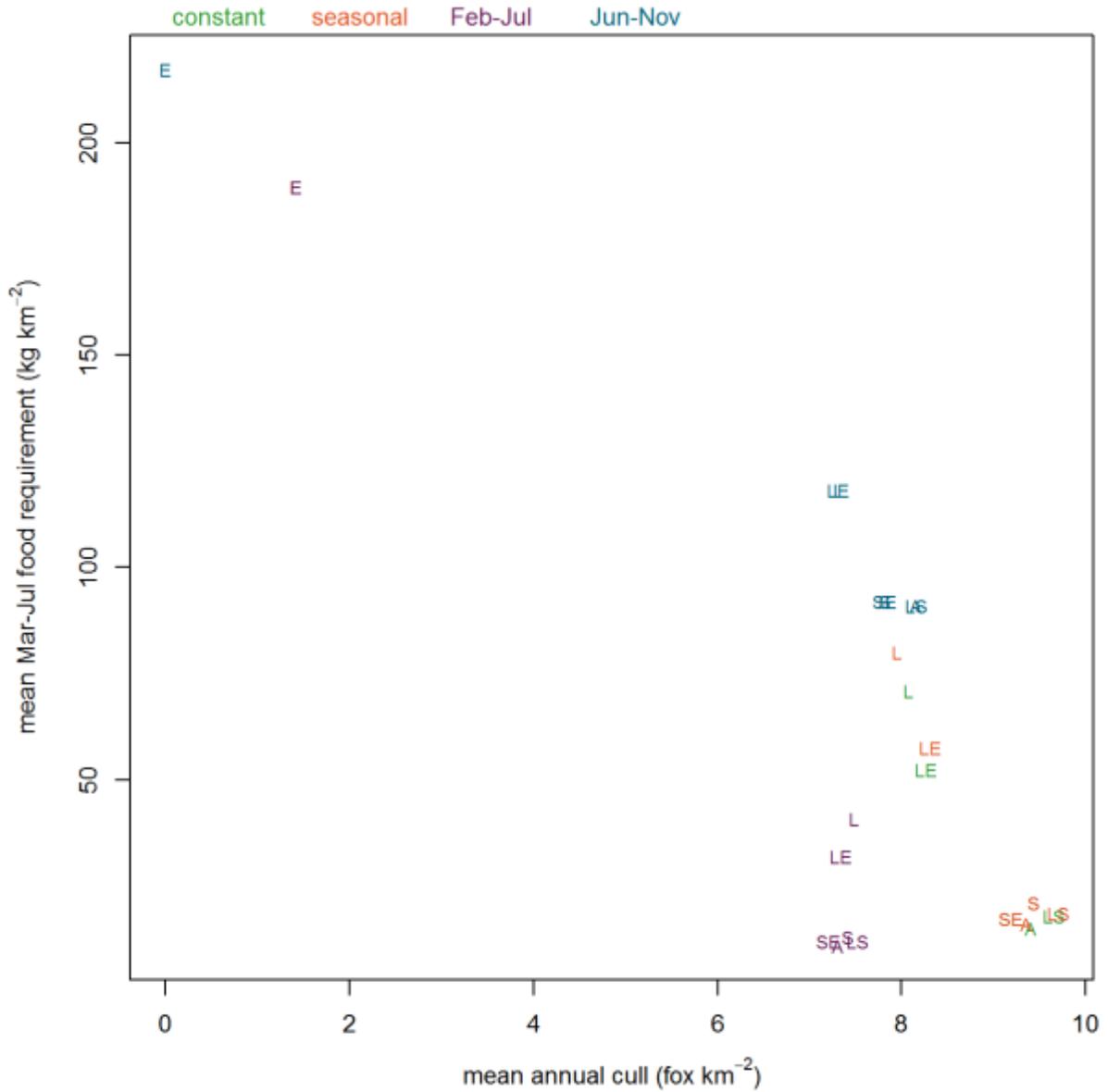


Figure I.2. Trade-offs between the effectiveness of different combinations of culling methods at reducing the food requirement during the nesting period and the number of foxes which must be killed annually to achieve this level of control on the NYP estate. Letters refer to each culling method (or combination thereof): L = lamping, S = snaring, E = cubs killed at earths, A = all methods. Results are from open-loop MSE and are shown under the maximum levels of effort for each method.

Appendix J Sensitivity to assumptions on other estates

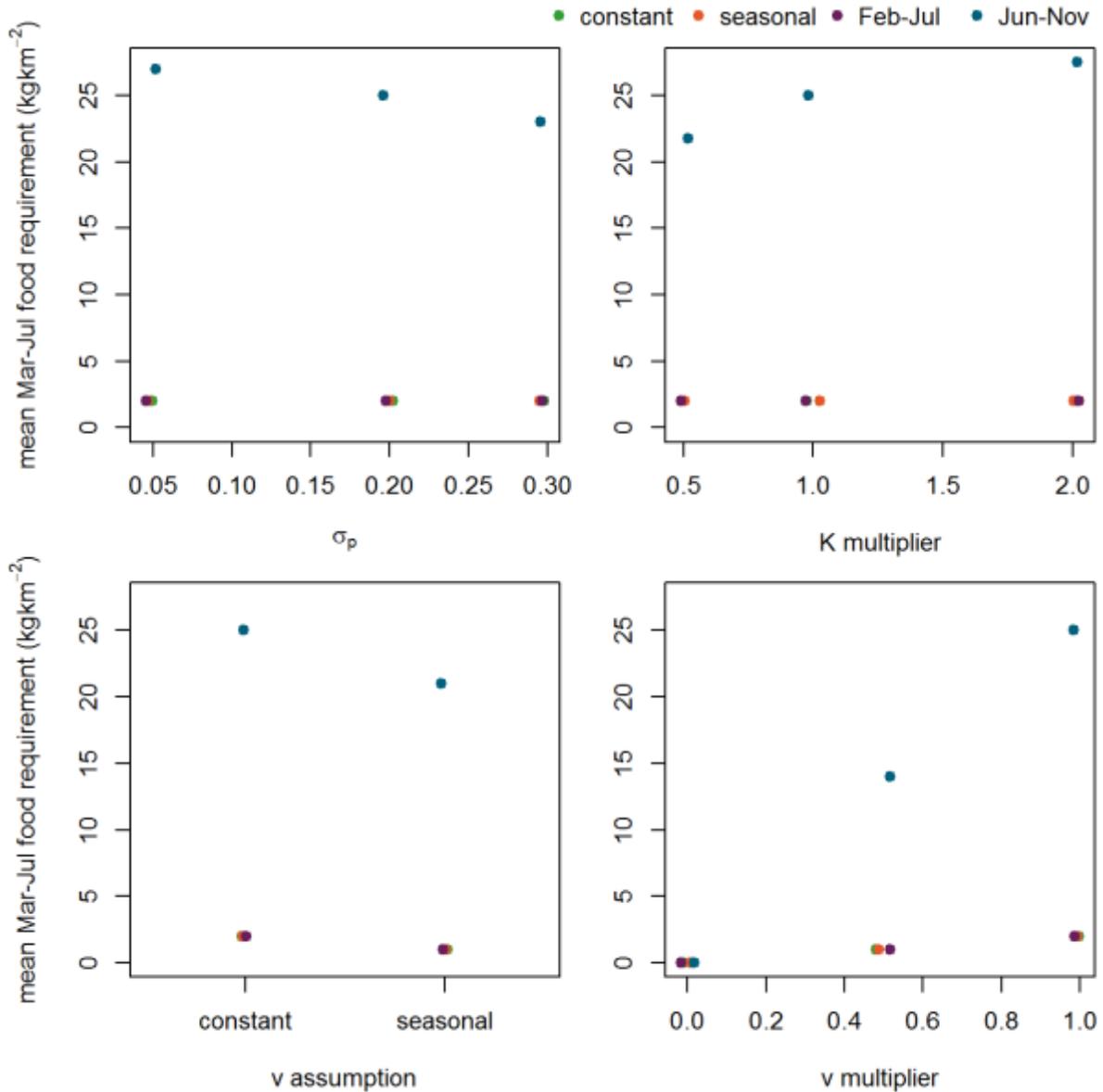


Figure J.1. Sensitivity of results on the VAR estate to different assumptions about the standard deviation in process errors (σ_p); the effect of assuming that immigration is a constant process throughout the year or is a seasonal process that occurs during the fox dispersal period; the effect of a higher or lower carrying capacity; and the effect of lower or zero immigration. Results are from open-loop MSE and are shown under the maximum levels of effort for all methods. Points are jittered around the x-values in each panel so that underlying points can be seen.

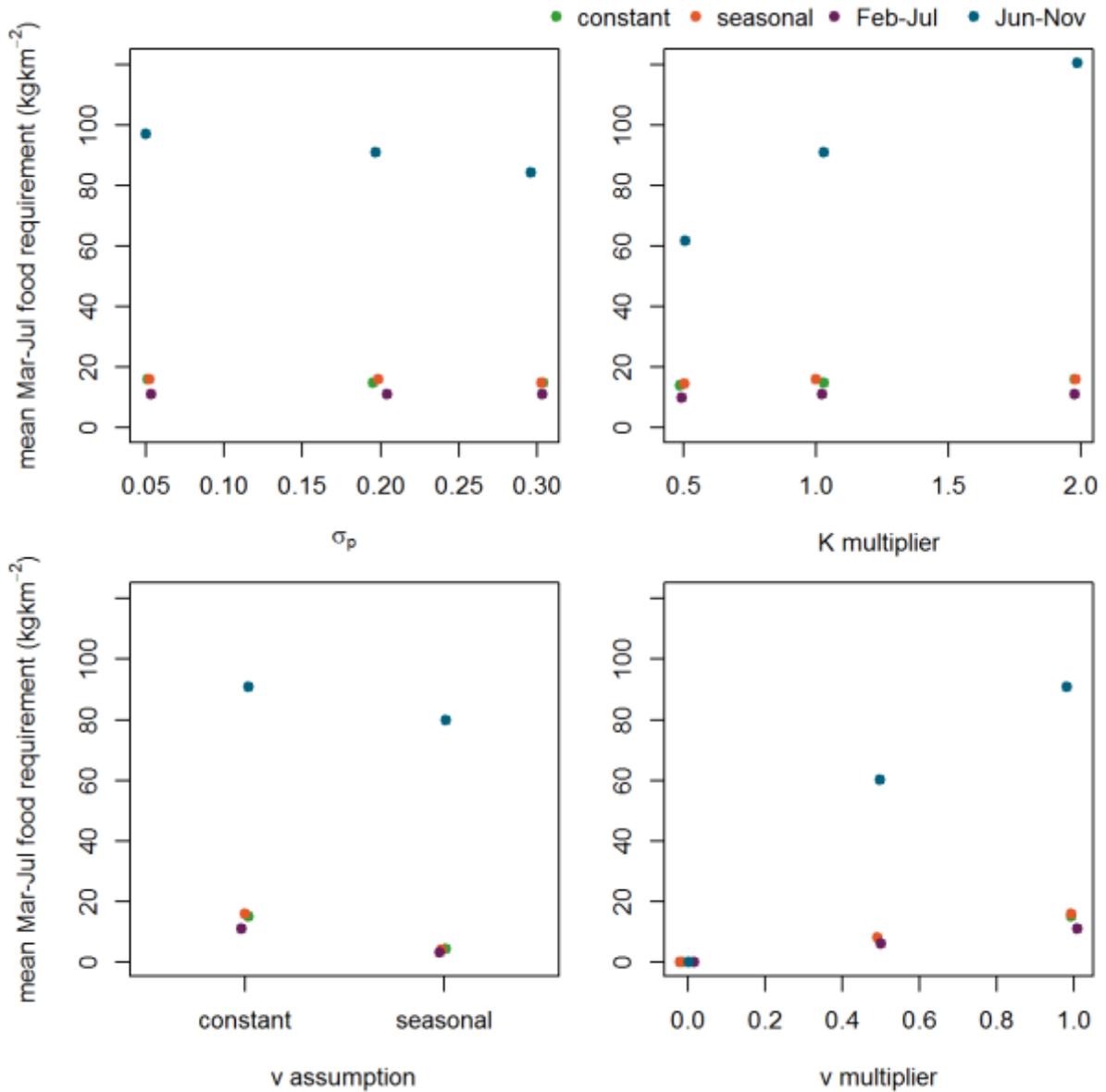


Figure J.2. Sensitivity of results on the NYP estate to different assumptions about the standard deviation in process errors (σ_p); the effect of assuming that immigration is a constant process throughout the year or is a seasonal process that occurs during the fox dispersal period; the effect of a higher or lower carrying capacity; and the effect of lower or zero immigration. Results are from open-loop MSE and are shown under the maximum levels of effort for all methods. Points are jittered around the x-values in each panel so that underlying points can be seen.

Appendix K Effect of feedback on other estates

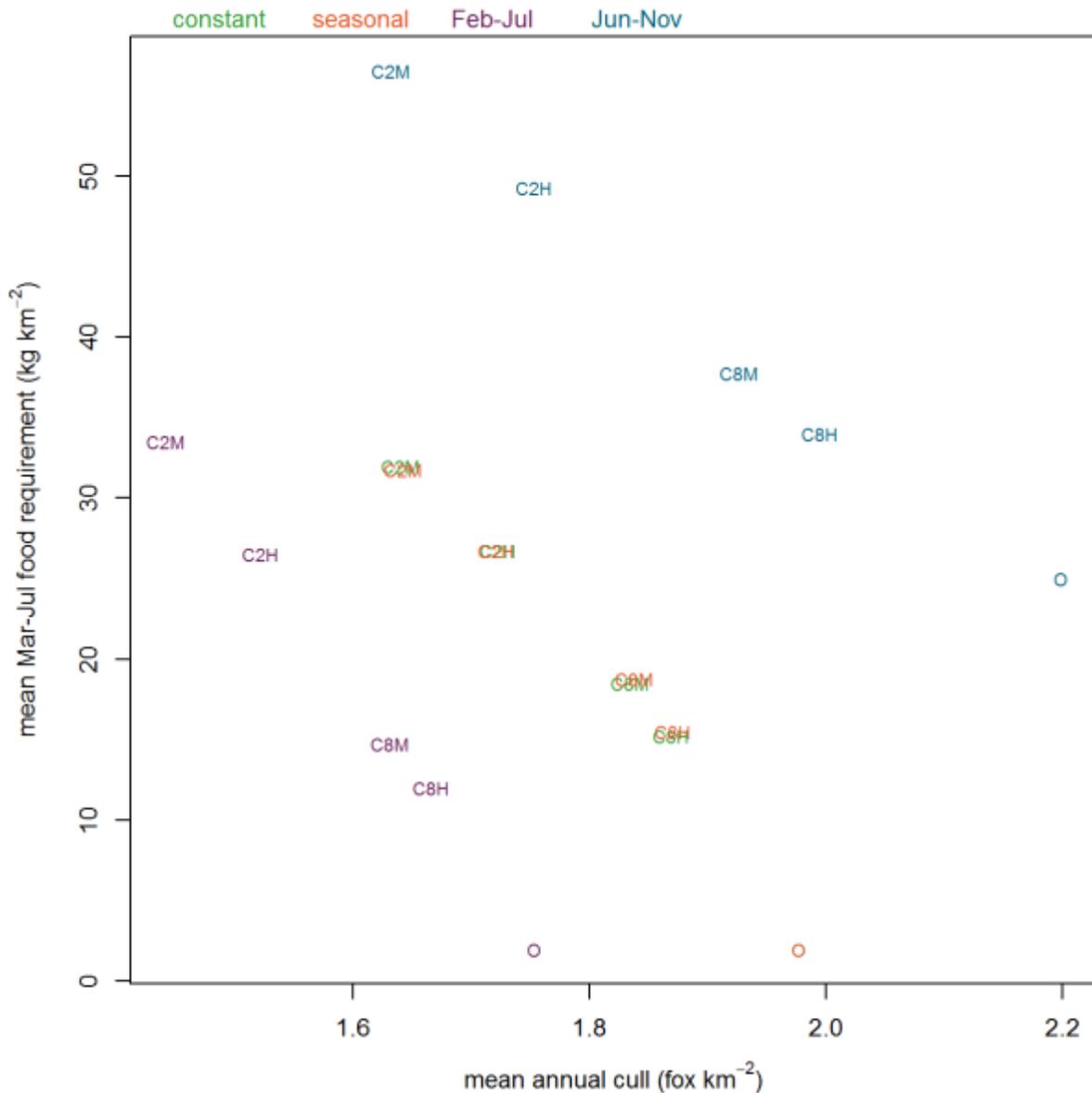


Figure K.1. Trade-offs between the food requirement during the nesting period and the number of foxes which must be killed annually to achieve this level of control under open-loop (O) and closed-loop (C) feedback on the VAR estate. For closed-loop options, numbers 2 or 8 refer to the number of search hours per week, letters M or H refer to the probability of finding scats if present (Medium = 0.5, High = 0.8). Results are shown under the maximum levels of effort for all methods.

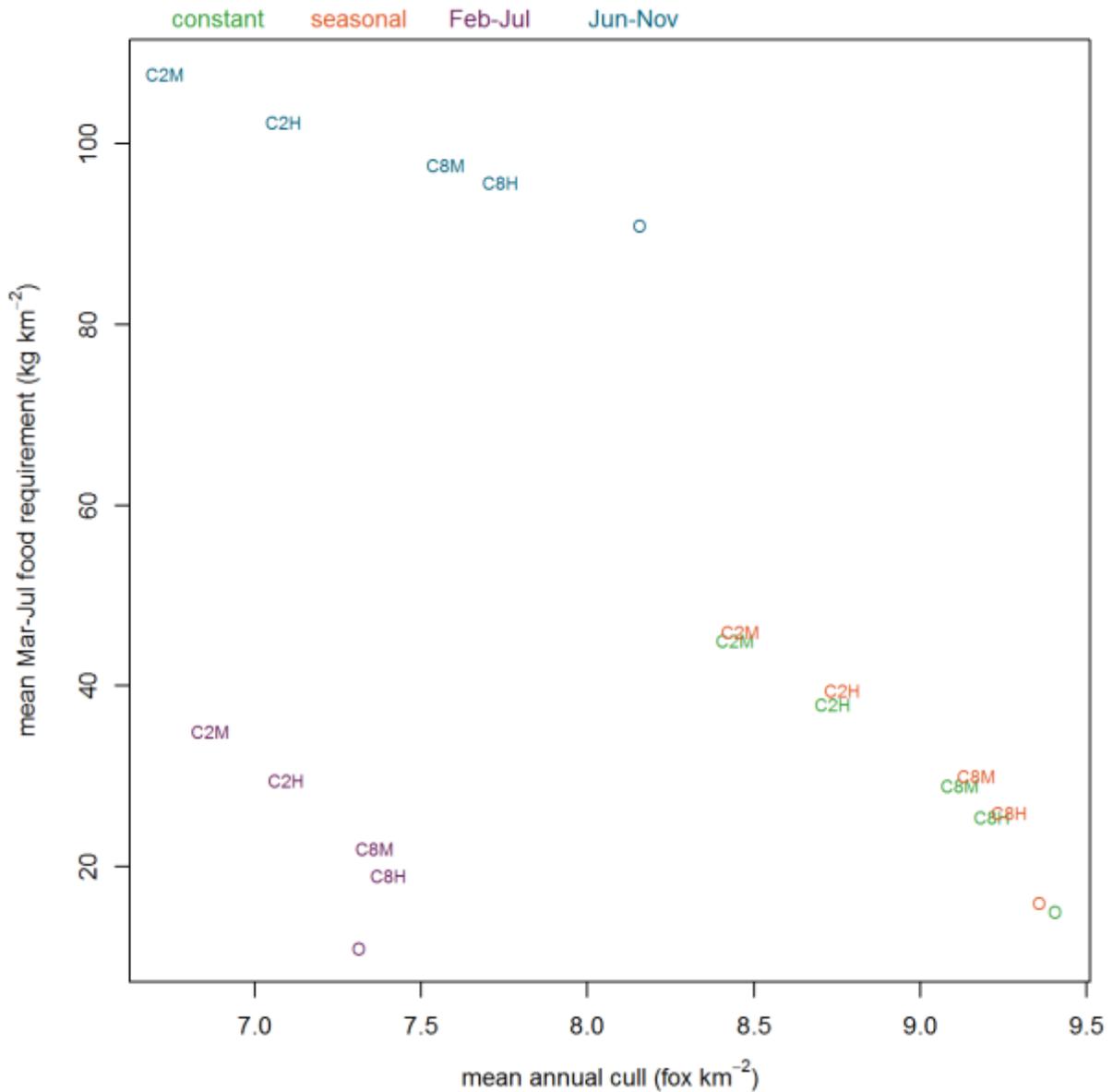


Figure K.2. Trade-offs between the food requirement during the nesting period and the number of foxes which must be killed annually to achieve this level of control under open-loop (O) and closed-loop (C) feedback on the NYP estate. For closed-loop options, numbers 2 or 8 refer to the number of search hours per week, letters M or H refer to the probability of finding scats if present (Medium = 0.5, High = 0.8). Results are shown under the maximum levels of effort for all methods.