IMPACT OF HUNTING ON SNOWSHOE HARE POPULATIONS IN NEWFOUNDLAND

by

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ABSTRACT

Snowshoe hares were introduced to Newfoundland between 1864 and 1876 to provide food and hunting opportunities. At that time, Newfoundland, an island, had no small game species. Today, snowshoe hares are still mainly hunted for food, particularly in rural areas. Harvest management for snowshoe hare has changed very little in Newfoundland since it started in 1879, with unlimited harvest allowed from October to February each year. Snowshoe hares were in low numbers in Newfoundland from 1979 to 1995, and many hunters believed that the unlimited harvest was depleting the hare populations.

Monitoring the effects of harvesting on snowshoe hare abundance is an arduous task, requiring monitoring effort throughout an entire hare cycle. I developed a modified, Lotka-Volterra predator-prey model to help with this task. Model parameter values were taken from the Kluane Boreal Forest Ecosystem Study. Harvesting applied to the model was derived from Newfoundland harvest statistics for 1965 to 1999. Harvesting lengthened the cycle period, which was directly related to the proportion of the population harvested at a cyclic low. Model parameters were tested for sensitivity.

Changes to snowshoe hare abundance within a hunting season were monitored using mark-recapture techniques. I live-trapped hares through a hunting season on two control (non-hunted) and two hunted grids from September 1999 to March 2000 during a cyclic peak. Population estimates were calculated using a Jackknife estimator (CAPTURE). Substantial declines were seen between September and January in both hunted areas, 46% and 77% of the fall populations, while the control areas remained
stable at 91% and 98%. There was some recovery in the population following the end of harvesting that is unlikely to be due to immigration. Abrams' (1993) theory of adaptive antipredator behavior was discussed. Both hunted populations recovered from harvesting by the following fall. Declines in population estimates of September 2001 compared to September 2000 indicated that the population was entering a cyclic decline.

Population estimates based on fecal pellet counts can be used as a cheaper alternative to live-trapping for monitoring snowshoe hare populations. For pellet counts in the Newfoundland forest, I found that the most efficient plot shape of those tested was a 10x150 cm rectangle. Pellets remained intact for at least 1 year but disappeared into the moss when it was the main ground cover.

Management of snowshoe hares should include a regular monitoring program through extensive fecal pellet counts that have been calibrated to live trapping efforts. At times of population lows in the snowshoe hare cycle, harvesting should be reduced.
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Chapter 1
Management of snowshoe hare populations

Background

Wildlife management began in Europe and, by the 18th century, management policies simply divided up the few resources that were left (Gilbert and Dodds 1992). At the same time, Europeans were reaping more and more from the New World's vast wilderness, both on the land and in the sea (Lavinge et al 1996, Mahoney 1999). By the 20th century, a noticeable decline in many exploited populations in the United States and Canada sparked the beginning of wildlife management or, more correctly, harvest management. The main purpose was to control human-wildlife interactions, either as regulations to limit exploitation or to reduce problems with wildlife; generally species that were not harvested were not managed (Gilbert and Dodds 1992, Lavinge et al 1996). Today, wildlife management goals have expanded to include conservation of all wild species and their habitats. Despite this broadening of views, the main focus of harvest management is still large game (e.g., moose, caribou, deer), while policies for small game (e.g., snowshoe hare, grouse, cottontail rabbits) are less restrictive, with only a fraction of the enforcement effort.

Management policies for snowshoe hare harvesting, the focus of this report, have been governed by the fact hares have a high fecundity rate—1 female produces 16 leverets per year (Hodges 1999)—and the assumption that populations are relatively unaffected by hunting (Gilbert and Dodds 1992). As a result, little effort has been put into actively managing the harvest. Agencies establish long hunting seasons of 3 to 5 months, and set bag limits that are
likely too high to effectively control harvesting. Caughley and Sinclair (1994) called this the ‘traditional’ mode of management, as it is mainly based on ‘personal experience and received wisdom’. Thus, scientific justification for this approach does not exist and all we can say is that it appears to work, because the hunted populations have not gone extinct.

The wisdom of this approach is debatable (Lavinge et al 1996). However, Caughley and Sinclair (1994) point out that when little is known about the population dynamics of a harvested species, the traditional mode is often the best approach to take, because if managers start manipulating harvest strategies without sufficient background knowledge, something is likely to go wrong. Historically, this may have been true when much of the land was not utilized by humans and acted as refugia for wild species. Today, with humans continuously moving into wilderness areas, with forest harvesting providing hunters access to new areas, and with the advent of all-terrain vehicles, hunted species are more vulnerable to overharvesting than ever before (Taylor and Dunstone 1996, C. Walters pers. comm. 2000).

Changes to a hunted population may occur through 5 mechanisms (Figure 1.1). Snowshoe hare populations receive new animals through immigration of animals from other populations and, during the breeding season, through reproduction. Animals are removed from a population by natural mortality, which is mainly predation, emigration of animals to other populations and hunting.

Hewitt (1921) stated that ‘a species of animal must not be destroyed at a greater rate than it can increase’ (p. 121). Seton, a naturalist and an important figure in the conservation movement of the Theodore Roosevelt era, believed that ‘no wild animal can stand a heavier drain [harvest] than 20 per cent per annum of its total population numbers’ (Allen 1938: p.378). However, Allen (1938) reported a harvest of over 50% of a cottontail rabbit population each fall
without impact on the next year's population. Pepin (1987) reported an annual harvest of 25-46% for brown hares on 650ha farmland in France. As with the snowshoe hare, the accepted belief is that the reproductive potential of these species will compensate for hunting losses and that immigration rescues locally depleted populations. The problem with determining what level of harvesting is sustainable has always been the need to harvest beyond biological sustainability, and then look back with hindsight (Walters 1986).

With the levels of hunting reported by Allen (1938) and Pepin (1987), hunters can be equated with a major predator and, as such, are strong competitors with the natural predators. Heavy harvesting of "keystone species" such as the snowshoe hare may have important effects on other species in the system. Research by Krebs et al (2001b) on various fauna and flora components of the boreal forest ecosystem show the importance of the community as a whole, and the domino effect that may occur when a keystone species declines. Wildlife managers have become more cognizant of community or ecosystem effects from harvesting a single species. This acknowledgement of interrelationships between harvested species and the other species in the community begs the question, *can we continue to assume that harvesting needs no regulation?* Recently, management agencies in Newfoundland and Labrador (this study), Nova Scotia (M. Bordeaux, pers. comm. 2000; Eaton 1993) and St Pierre-Miquelon (France, M. Morisson, pers. comm. 1999), where snowshoe hares are an important food supplement, have begun to question the wisdom of current policies of minimum management.

**History of Snowshoe Hare in Newfoundland**

Snowshoe hares are not native to Newfoundland, an island on the east coast of Canada (Figure 1.2). They were introduced from Nova Scotia and distributed throughout the island.
between 1864 and 1876 by local Magistrates as a food supplement (Dodds 1960). Rabbits, as they are locally called, quickly entrenched themselves into the lives of both Newfoundlanders and the island’s fauna and flora.

A review of newspapers and government document by Dodds (1960) indicated that the snowshoe hare population increased drastically from 1896 to 1912, then sharply declined and began typical cyclic fluctuations in 1920 with peaks in 1920, 1931, 1942, 1952, 1959, 1969 and 1976 (Dodds 1960, Bergerud 1983). While the occurrence of peaks appeared consistent with other areas of Canada, the population high for Newfoundland in 1976 was not. At this time, other areas were experiencing a cyclic low in hare populations. The lynx harvest data, which show the highest harvests in the early 1980’s, however, suggest that hares may have stayed high, at least in some areas, right up until 1979. O’Donoghue et al (2001) indicated that there is typically only a one-year lag between cyclical peaks in numbers of hares and numbers of lynx. However, this lag may appear 2-3 years after the hare peak in lynx harvest statistics, because lynx become more vulnerable to harvest during the cyclical decline (M. O’Donoghue pers. comm. 2001). The late 1970’s peak was then followed by a persistent low to 1996 (O. Forsey, pers. comm. 1999). There is some evidence of a peak between 1988 and 1990. Pellet plot data from Thompson and Curran (1993) and a decreasing harvest indicated that hare abundance dropped from 1990 to 1992. However, hares were rarely observed during the late 1980’s. In addition, the trapping season for lynx was closed from 1987 to 1989 due to low numbers, and harvesting remained relatively low even after the trapping season re-opened in 1990 (Figure 1.3). After 1995, there was an increase in the number of snowshoe hares harvested in Newfoundland (Figure 1.3). By spring 2000, snowshoe hares were seen everywhere; road kills were quite
common and they became pests in commercial and ornamental gardens. Lynx harvesting has also shown a large increase.

The first regulation governing harvest of snowshoe hares was a bill passed in 1864, making the killing of snowshoe hare illegal and, in 1869, a £20 fine was also instated. This was to allow time for the populations to become established. Fifteen years after the initial introduction, the first hunting season opened in 1879, which ran from September 1 to February 28, and there was no bag limit. In comparison, current harvest management involves a hunting season from about October 10 to February 28 and, in 1997, the first bag-possession limit of 40 hares was imposed on Newfoundland hunters.

A commercial canning operation opened on the west coast of Newfoundland in 1934. This industry provided the residents of the province, particularly in the urban areas of St. John’s, Corner Brook and Grand Falls, with freshly canned snowshoe hare bought from local ‘rabbit’ catchers of all ages. During years of high snowshoe hare populations, as many as 250,000 hares were processed (Dodds 1960). Although the industry was closed just before Newfoundland joined Canada in 1949, Newfoundlanders retained the right to sell snowshoe hares, and the tradition of canning ‘rabbits’ for personal use is still popular. As in the past, the price for a brace (or pair) of ‘rabbits’ is strictly determined by supply and demand, a brace can fetch from $2 during a cyclic high in populations to $8 at a low. Dodds (1960) referenced the law of diminishing returns such that, as hare populations become low and hunting less successful, the number of hunters will decrease. However, that is likely to help support those interested in the commercial aspect of harvesting because the demand for hare meat still exists.

Snowshoe hare harvesting in Newfoundland is primarily for food, rather than sport. Hunters employ one of two techniques to harvest hares. Over 80% of the hunting population,
use snares, a wire hoop placed in the path of a hare ‘run’, and about 20% of hunters, generally from the urban centre, use dog(s) and rifle. Snaring is a more effective hunting technique, though take will depend on the number of snares set and the number of hares in the area. We estimated that for the 1998 hunting season 22,000,000 snare-nights were used to capture about 800,000 snowshoe hares (McGrath unpubl. data. 1999) across the 5,500,000 ha of forested landscape.

Over 30,000 small game licences are sold each year in Newfoundland. Hunter returns indicate that while this licence covers snowshoe hares, grouse and ptarmigan harvesting, more than 90% of hunters are taking snowshoe hares, and they are taking an average of 38 hares each. When combined with the commercial sale of hares, the resulting hunting pressure is substantial. The annual harvest from 1966 to 1992 ranged from 200,000 to 2,000,000 hares with the average just over 1,000,000 (Figure 1.3). While the rate of small game returns has been low at 5%, a recent mail-out questionnaire and telephone survey confirmed that the return results are representative of the overall hunt in Newfoundland (M. McGrath 1996, M. O’Donoghue pers. comm. 1999). Despite the observed decline in hare populations after 1976, harvesting levels remained high until 1991, possibly due to increased hunting effort and high prices paid for hares. By 1992, a sharp decline in the annual harvest occurred and, in 1995, the harvest was estimated at only 82,000 hares. With snowshoe hare harvest at a record low, hunters began to express concern over the commercial sale of hares and the high harvest that resulted from the current regulations.

Historically, a low in the snowshoe hare cycle would have meant hard times for many Newfoundlanders – the canning industry, food for families, selling fur, and trapping of lynx and fox are all driven by the hare cycle. Before the completion of the Trans-Canada Highway and
other major highways in mid-1960s to mid-1970s, many rural areas of Newfoundland were only accessible by boat. As a result, the supply of meat from domestic animals was often unavailable during the winter months, and capturing wild game was a matter of survival. Today, many Newfoundlanders still supplement their dinner plates and pocketbooks with snowshoe hares.

**Other Forest Species**

The introduction of snowshoe hare into Newfoundland must have had a profound impact on the current fauna of the island. In the late 1800s, the forest community of Newfoundland was home to the meadow vole and possibly a small number of arctic hare (*Lepus arcticus*). There has been a debate about the occurrence of arctic hare in the forested area of Newfoundland prior to the introduction of the snowshoe hare (Cameron 1958, Dodds 1960, Bergerud 1967 but also see Mercer et al 1981). The house mouse and Norway rat had been introduced in 1500’s but were likely limited to areas around communities. In contrast, predators were quite plentiful, including the red fox, Newfoundland marten, Newfoundland wolf (extirpated by 1922), Canada lynx, great horned owl, bald eagle, goshawk and many other raptors (Figure 1.3). The traditional predator of the snowshoe hare, the lynx, was first recorded in 1820, but it remained at low numbers until the snowshoe hare arrived. Following the introduction of the snowshoe hares, the lynx population exploded and, in 1900, a “Lynx Extermination Bill” was introduced to control the high lynx population (Dodds 1960). Trapping of lynx for its pelt probably began around this time, although the current records only cover the period from 1963 to 2000 (Figure 1.3). From 1987 to 1989, lynx harvesting was closed, due to low populations, and although the season reopened in 1990, the harvest remained relatively low until 1996. By the fall of 2001, lynx had once again reached nuisance status with many reports of lynx within rural communities.
Additional animals introduced intentionally or by accident since late 1800s include the spruce and ruffed grouse, moose, deer mouse, red-backed vole, red squirrel, and mink (Figure 1.4). Also, in 1985, the eastern coyote made its way from Nova Scotia and has since established itself throughout the province, although its population abundance has not been enumerated. The coyote was found to be a major predator of snowshoe hare in Yukon territory (O’Donoghue et al 1997).

Research Objectives

Regulations for wildlife management in North America began in 1600s with management of large game species becoming increasingly more complex (Gilbert and Dodds 1992). Regulations for harvesting of large game animals target individuals of specific age and sex, to offer more hunting opportunities while still protecting the viability of the population. Despite advancements in population theory and manipulation, the harvest management of small game has remained virtually unchanged since it began. I have found no studies that examined the effects of hunting on snowshoe hares. Related work such as movement and removal studies can offer some insight into the potential effects of hunting, but they cover relatively small areas compared to those searched by hunters.

The objective of my research was to explore the impact hunting might have on snowshoe hare populations in Newfoundland. Chapter 2 examines the predicted effects of harvesting on a cyclic population using a modified Lokta-Volterra model. Chapter 3 discusses the observed effects of harvesting within a hunting season and between consecutive hunting seasons. Populations of hares on two hunted and two non-hunted grids were monitored before, during and after hunting using mark-recapture techniques. Chapter 4 reviews the use of pellet counts to
monitor hare populations in Newfoundland. Finally, Chapter 5 summarizes the results on the impact of harvesting on snowshoe hare populations in Newfoundland, and suggests recommendations for future management.
Figure 1.1: Snowshoe hare populations receive new animals from reproduction and immigration including natal dispersers moving into the area. Animals are removed from a population by natural mortality, emigration including juvenile hares leaving the area and hunting.
Figure 1.2: The location of the four trapping grids (Terra Nova National Park, Port Blandford Woodlot, MUN Woodlot and Butter Pot Provincial Park) within eastern Newfoundland. The grey shaded area represents the forested region of Newfoundland (about 5.5 million ha) and the habitat available to snowshoe hares. The land mass of Newfoundland is approximately 11 million ha. St Pierre and Miquelon (south of the Newfoundland) is a territory of France. Inset is Canada with the provinces and territories labelled.
Figure 1.3: Annual harvest of snowshoe hares (from hunter returns), 1966-1999, and lynx (from pelt registrations), 1963 to 2000, in Newfoundland. The lynx season was closed from 1987 to 1989. The recorded harvest were accidental captures in fox snares.
Figure 1.4 Diagram of the small prey species of the boreal forest of Newfoundland and their predators. Arrows are drawn to indicate those species that may prey on snowshoe hare. The other species are listed as possible alternative prey. A variety of songbirds also occur with the forest but are not included here. The heavy boxes indicate indigenous species. The I = year indicates the year a species was introduced. RE refers to range expansion of the eastern coyote. The Newfoundland wolf was extirpated by 1922.
Chapter 2

Hunting impacts on snowshoe hare population abundance: Models

Introduction

The effects of harvesting on snowshoe hare populations are unknown, but the working assumption is that a species as widespread and prolific as snowshoe hares cannot be hunted to extinction. Therefore, resource managers have put little effort into management of snowshoe hares and have generally focused on larger game that are known to be susceptible to overexploitation. However, snowshoe hare hunters in Newfoundland recognize that areas are often ‘trapped-out’ and move to other hunting grounds for the rest of the season. Here I consider whether harvesting can have long-term implications for snowshoe hares or their predators?

Monitoring the effects of harvesting on a wild population is not an easy task, and it will often take years for the consequences to be realized. Thus, the development of models to assist with population monitoring has become important. Models only approximate the dynamics of parts of any natural system, and we should not be arrogant in our belief that we can duplicate nature exactly. A model’s usefulness is in helping to assemble our existing knowledge, forcing us to organize that knowledge into a structured framework, identifying gaps in our understanding, and describing the best parameters to monitor (Brown and Rothery 1993). Then, as we confront the model with data, we can further advance our understanding of the interactions between the model parameters, or, more likely, we better realize the complexities of nature and our ignorance of it.
There are many published models or software programs that can be used to model the impact of harvesting populations. However, in using a pre-existing model, the modeler is limited by the structure of the model, which may not have been designed to answer the questions now being asked. The model may be more complex than required or not complex enough. Furthermore, the modeler is often ignorant of the hidden assumptions and sensitivities within the existing model. Here my objectives are:

1) to examine the potential impacts of harvesting snowshoe hares at rates similar to that estimated for Newfoundland for 1965 to 1999 on a cyclic population;
2) to forecast long-term impacts of high harvesting rates on snowshoe hare populations.

It is predicted that harvesting can have an impact on snowshoe hare populations, especially at a cyclic low. Harvesting during a low is expected to lengthen the low phase and increase the cycle period.

Methods

I began by building a Lotka-Volterra logistic growth model for snowshoe hare and lynx using data from the Boreal Forest Ecosystem study near Kluane Lake, Yukon (Krebs et al 2001b). I used parameter estimates from work in the Yukon, because it is the most complete data set available. The basic unit in the model was density (number of hares and lynx per hectare). The model produced cyclic populations for both hares and lynx, with a cycle period of 10.2 years (Figure 2.2a) and a 30-fold change for hare populations and 6.9-fold for lynx (O'Donoghue et al 1997).
Once the model was built, I tested its behavior when snowshoe hares were harvested at levels similar to that estimated for Newfoundland from 1965 to 1999. In terms of model behavior, I looked for changes in the cycle period and pattern, the peak size of populations for hare and lynx, and the amplitude.

**Model development**

Model development began with a Lotka-Volterra logistic growth model fashioned after Gotelli (1998) and Walters (1986, pers. comm. 2000), where the change in populations were calculated as (births – deaths). The formulae are presented below.

Births, deaths and harvest were applied at each time step in a continuous interval approach. In terms of births, the highest birth rate observed at Kluane was applied, and growth was limited by using a density-dependence rate of increase such that the population change was negative once the population exceeds the carrying capacity. Predation is responsible for more than 90% of snowshoe hare deaths, with coyotes and lynx being the main predators (Hodges 2001). Therefore, the only natural mortality factor used in the model was predation. To simplify the model I used a single predator, the lynx. In a detailed study of predation, O'Donoghue (1998) suggested that lynx response to changes in snowshoe hare density can be defined by a Holling Type II functional response equation (Gotelli 1998). I modeled both prey mortality and predator productivity by using this equation (Holling 1959), which considers the predator’s consumption of prey limited by time spent searching for and handling prey.

Lotka-Volterra models modified by incorporating factors such as functional responses by predators are often unstable (Gotelli 1998). Therefore, a common practice
to prevent the collapse of the model is to put a lower limit on prey density, which acts as a refuge at very low abundance thereby preventing extinction (Gotelli 1998). Abrams and Walters (1996) took a more realistic approach. They assumed there was always a portion of prey ‘in a refuge’ that was invulnerable to the predator, because of either its spatial location or its physiological or behavioral state (Figure 2.1). Prey, such as snowshoe hares, may switch from being vulnerable to invulnerable simply by moving from a foraging area, where they are exposed to predators, to cover that the predator cannot penetrate. The invulnerable prey component acts to stabilize the predator-prey interactions. Observations from live trapping of snowshoe hares indicated that a portion of the hare populations was invulnerable to hunting efforts by humans (T. Joyce unpubl. data), and therefore harvesting was only applied to vulnerable prey.

**Formulae for the Model**

The model incorporated direct affects between prey and predator through a feedback loop. It assumed that changes in prey numbers \(dN/dt\) were related to the predator abundance, and changes in predator numbers \(dP/dt\) depended on prey abundance. The following relationships describe predator and prey abundances and are described below:

\[
\begin{align*}
    dN/dt &= r*(1-N/k)*N - ap * V_N * P/(1 + ap*V_N*h) \cdot \text{harvest} \quad \text{and} \quad N_{t+z} = N_t + z*(3*dN/dt+z - dN/dt)/2 \\
    dP/dt &= et * ap * V_N * P/(1 + ap*V_N*h) - dp*P \quad \text{and} \quad P_{t+z} = P_t + z*(3*dP/dt+z - dP/dt)/2
\end{align*}
\]

Where \(dN/dt\) = change in prey over time; \(dP/dt\) = change in predator over time; \(N\) = prey per ha; \(P\) = predator per ha; \(z\) = time step; \(r\) = prey rate of increase; \(k\) = carrying capacity; \(ap\) = rate of search by predator; \(V_N\) = vulnerable prey; \(h\) = predator handling time; \(et\) = predator efficiency; \(dp\) = predator mortality rate.

The basis of the formulae \(dN/dt\) and \(dP/dt\) was a logistic growth model where the change in population was calculated as births - deaths. \(N\) was the number of prey per ha
and \( dN/dt \), the change in prey numbers on a very short time scale (1/10 of a year). Likewise, \( P \) was the number of predators and \( dP/dt \), the change in predator numbers. All values and descriptions for parameters used in the model are given in Table 2.1. For prey birth, the highest rate of increase, \( r \), observed in the Kluane study was used (18.9 leverets per year), and growth was limited by the density-dependent rate of increase and multiplied by population size \([r*(1-N/k)*N]\). The Kluane estimate was higher than Dodds’ (1965) estimate of 13.7 leverets per year for snowshoe hares in Newfoundland during a cyclic increase and peak. Dodds examined follicular development (Green and Evans 1940) in the ovaries of 219 hares.

The prey death component in the model incorporated the interaction between predator and vulnerable prey using the Holling’s disk equation \([ap*V_N* P/(1+ap*V_N*h)]\) (Holling 1959). Time spent searching for prey \((ap)\), which is often referred to as search efficiency, was based on speed of travel \((m/hr)\) multiplied by the reactive distance \((m)\) of the predator and the successful rate of capture (Mowat et al 1999, O’Donoghue et al 1998). Handling time was derived from an estimate of 45 minutes to consume a hare. Conversion efficiency \((et)\), the rate at which predators convert prey consumption into offspring, used in the \( dP/dt \) equation was calculated based on a pair of lynx eating 2.4 hares per day and having 4 young per year. The parameter \( V_N \) was a complex formula using the flow of prey in \((v1)\) and out \((v2)\) of the vulnerable pool, as well as handling time, search efficiency, and the abundances of hares and lynx. Research completed in Kluane on hare mortality indicated that a large proportion of the hares were vulnerable to predation at any given time (Hodges et al 2001). For this model, I used a ratio of 30 vulnerable \((v1)\) to 1 protected \((v2)\). The model was checked for sensitivity before
applying harvest, by changing each parameter individually and recording effects on the predator and prey abundances and cycle period.

---

**Applying harvest to the model**

To confront the above predator-prey model with the harvest data for Newfoundland, I used sum of squares approach (Hilborn and Mangel 1997). For my purposes here, I refer to the harvest data for Newfoundland 1965 to 1999 as the observed data. Newfoundland data are estimated from licence sales and harvest reported by questionnaire respondents. I defined the sum of squares, as the difference between the natural logarithm of the observed data divided by the predicted data and its mean (C. Walters pers. comm. 2001). The best-fit harvest occurred when sum of squares was minimized. This was accomplished by allowing the predicted data to vary until the minimum value of sum of squares was found. The resulting predicted data was the best fit for the observed harvest within the predator-prey model used. Sum of squares does not make assumptions about how uncertainty enters into the model. The sum of squares value provided no information in terms of confidence in the results.

Within the model, predicted harvest was removed from the vulnerable prey. The computations required to find the predicted harvest were completed using SOLVER tool in EXCEL® computer software. Within SOLVER, I constrained the predicted harvest to between carrying capacity, K (Table 2.1), and 1% of the vulnerable prey to ensure some hunting always occurred.
Results

Observed harvesting data existed for 3 complete cycles, 1965 to 1999. The cyclic behavior of the predator-prey model continued after the application of the predicted harvest (Figure 2.2b) but there was a decay in the peak density reached as time progressed. The peak density for 1974 was 2.11 hares per ha; 1987, 1.97; 1998, 1.85, and 2008, 1.79 (Figure 2.2c). Without harvesting the peak reached a consistent 1.8 hares per ha after 1973. The low densities for the models with and without harvest remained stable at 0.06 hares per ha, except for the model with harvest from 1967 to 1970 when density declined to 0.03 hares per ha. The progressive decay in peak density resulted in a slightly smaller amplitude at each peak. There was little visible change in the smooth, cyclic pattern despite the heavy harvest of vulnerable hares. This resulted from using a small time step (1/10 year) and the continuous interval method where births and harvest were spread over an entire year. The period of the cycle was variable and related to the proportion of the vulnerable prey harvested; this will be discussed in more detail below.

Predicted harvest provided a reasonable fit to the observed harvest for Newfoundland (Figure 2.3). However, it did not emulate the low that was believed to have occurred from 1979 to 1995. There were two large variations between the predicted data and observed data. From 1972 to 1974, the predicted harvest was much higher than of the observed (Figure 2.3). This is reflected in the proportion of vulnerable prey harvested at 89% (Figure 2.4), which resulted in an extended low from 1966 to 1971. The second variation occurred from 1979 to 1983 when the predicted harvest was much lower than the observed. After 1999, no observed harvest data were available and the
predicted data adopted a regular, smooth pattern dictated mainly by prey abundance. The cycle period was 10.4 years.

The predicted proportion of vulnerable prey harvested peaked on three occurrences in correspondence to three lows in the prey population, 1966.2 to 1970.9, 1979.5 to 1983.1, and 1990.9 to 1994.1 (Figure 2.4). The extent of these lows (x) is related to the proportion of vulnerable prey harvested (y) and can be described by a second order polynomial \[ y = 2.44x^2 - 0.268x + 3.00 \] with \( R^2 = 0.9996 \) (Figure 2.5).

Without harvesting, the mean low period length was 3.0 ± 0.19 years. Using this equation, 100% removal of the vulnerable prey component would result in a low period of 5 years.

The model proved to be sensitive to changes in several of the parameters tested. The modelled values are found in Table 2.1. Summary of the sensitivity analyses can be found in Appendix I. As the prey rate of increase increased, prey numbers per ha decreased, possibly due to the responding increase of predators per ha (Figure 2.6a). Increases in prey carrying capacity (K) followed by predator abundances indicated that the paradox of enrichment did not occur in this model (Figure 2.6b). An increase in predator search efficiency resulted in an increase in predators per ha and an a sharp, unexplained increase in prey per ha (Figure 2.6c). Increasing predator handling time resulted in asymptotic function for both predator and prey, with each reaching maximum density at 0.02 and 0.04 time per hare, respectively (Figure 2.6d). With predator conversion efficiency values less than 0.04 (Figure 2.6e), which equates to about 2.8 kits produced per lynx pair per year, the model ceased to cycle. Predator death rates did not have much of an effect on prey and predator abundances until the rate reached 0.8 (Figure
2.6f). However, it had a large impact on the cycle period. Low predator death rates resulted in epidemic-type cycles with the cycle period at 26 years, and hares still peaking about 2 per ha. Mortality of predators at or near 100% resulted in a cyclic population with a small amplitude (3-fold change) and a period of 9.5 years.

Discussion

As predicted, harvesting of snowshoe hares resulted in modifications to the predator and prey population cycles. While the cyclic pattern was maintained, there were changes to the cycle period, amplitude and peak densities for prey. The main findings were:

1) The predicted data provided a reasonable fit to the observed data, however, it did not emulate the low in snowshoe hares experienced in Newfoundland between 1979 and 1995.

2) Harvesting lengthened the cycle period. The lengthening of the cycle was directly related to the amount of harvesting of the vulnerable prey component of the population, at a cyclic low and can be described by a second-order polynomial function.

3) There was a slow, progressive decline in peak snowshoe hare densities under the harvesting regime presented, which resulted in declining amplitude.

4) The period of the lynx cycle mimics that of the snowshoe hare. However unlike the hares, lynx populations did not exhibit a decline in peak abundances.

5) The model was sensitive to small variation in the values of predator conversion efficiency and handling time.
6) Prey per ha was greatly influenced by predator search efficiency in a manner that appeared to be inconsistent with the general understanding of the predator-prey system. As predators became more efficient at searching for prey, prey abundances increased.

7) After 1999, the predicted harvest stabilized at a low proportion of vulnerable prey and was dictated by hare abundance.

Although the model did not reproduce the cyclic low experienced in Newfoundland snowshoe hare populations from 1979 to 1995, it did show that heavy harvesting at a cyclic low will extend that low. This has significant implications for snowshoe hare and lynx harvest management. If the purpose of harvest management is to provide people with opportunities for hunting and trapping, then it would seem prudent to decrease hunting pressure when snowshoe hare populations are low.

The model predicted a slowly decaying peak abundance as a result of harvesting. It is unknown if such would occur in a harvested population. Addressing this would require regular surveys of snowshoe hares through several cycles, as the inherent variability within population abundances would mask slight declines. It is unclear why the decline was observed in the peak abundances of lynx. However, in order for lynx to maintain itself in light of the fluctuating hare populations, slight changes in hare abundance should not have a measurable impact on lynx populations.

The high sensitivity of the model to the parameters predator conversion efficiency and handling time is troublesome (Figure 2.6d,e). In order to calculate predator conversion efficiency, I used mean number of hares eaten per day and mean number of lynx born per breeding pair. These parameters were sufficiently variable to crash the
model. There appeared to be a threshold value of 0.04, before which the model did not cycle. This was due to predator abundance being too low to have an effect on hares, whose abundance levelled out just below carrying capacity. After the threshold value was exceeded, the model did cycle with an amplitude consistent with the observed data from the Kluane Boreal Forest Ecosystem Study. Predator conversion efficiency was only used in the calculation of \( \frac{dP}{dt} \) where it had a large influence on the entire model. This sensitivity was not caused by the fact that, if a pair of lynx do not eat 2.4 hares per day the population would stop cycling. More likely, it was a consequence of using constant values for the parameters throughout the cycle and a single prey-single predator model.

Since handling time of prey has not been determined (O'Donoghue et al 2001), I made an arbitrary assumption about the time it takes a lynx to consume a hare. Due to the sensitivity of the model to handling time, there were few values possible and still have the model function. This parameter was used in the equations for change in prey over time \( \frac{dV}{dt} \), change in predators over time \( \frac{dP}{dt} \), and vulnerable prey \( V_N \). By varying the value of handling time in each equation individually, I found \( V_N \) insensitive to changes, while both \( \frac{dV}{dt} \) and \( \frac{dP}{dt} \) were sensitive.

The influence of increasing predator search efficiency on prey per ha was similar to increasing the harvest, in that the cycle period lengthened mainly due to longer cyclic lows (Appendix I). However, in this case, the prey were able to reach higher peaks while lynx populations were low. This did not occur for increased harvesting, as the hunters can more quickly respond to increasing hare numbers.
Due to the yearly variability of the harvest within Newfoundland it was not possible to predict future harvest estimates using the method described above. As a result, I was unable to directly predict long-term impacts of harvesting on snowshoe hare populations. I can predict from the model’s behavior, that snowshoe hare populations will be suppressed at cyclic lows when hunting pressure is high during that time. This will result in suppressed lynx populations as was observed in Newfoundland. From both the hunter trend data (Figure 1.3) and the model, I predict that snowshoe hares in Newfoundland will continue to exhibit cycles, they will rebound from these lows, and that the cycle period will be influenced by the amount of harvesting at cyclic lows.

**Summary**

Models can be an effective tool to study the impacts of harvesting on populations. I developed a modified Lotka-Volterra predator-prey model using parameter values from Kluane Boreal Forest Ecosystem Study. The application of harvesting to the model resulted in an increase in cycle period that was related to hunting intensity during the low period of the cycle. Testing of parameter sensitivity indicated that small variations in either predator conversion efficiency or handling time had a large impact on the model.
Table 2.1: Parameters descriptions and values per time step (1/10 year) used in the continuous interval predator-prey model with harvest. The main data source is Kluane Boreal Forest Ecosystem study (Krebs et al 2001b)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>r</td>
<td>Snowshoe hare rate of increase</td>
<td>1.89</td>
<td>Maximum reproduction is 18.9 leverets/yr (Hodges et al 2001)</td>
</tr>
<tr>
<td>K</td>
<td>Carrying capacity (hares/ha)</td>
<td>2.4</td>
<td>Peak density reached in the predator exclosure grid (Hodges et al 2001)</td>
</tr>
<tr>
<td>ap</td>
<td>Search efficiency of predator. Area searched by predator for prey- velocity (m^3/time step)</td>
<td>133</td>
<td>% successful capture * distance * speed (O'Donoghue et al 2001, Walters 1986)</td>
</tr>
<tr>
<td>h</td>
<td>Handling time of predator</td>
<td>0.03</td>
<td>Estimated time spent handling/eating (45min per hare)</td>
</tr>
<tr>
<td>et</td>
<td>Conversion efficiency. Rate prey are converted to predators (hares per lynx per time step)</td>
<td>0.05</td>
<td>4 kits per year for pair eating 2.4 hares/day (O’Donoghue et al 2001, Slough and Mowat 1996, Poole 1994)</td>
</tr>
<tr>
<td>dp</td>
<td>Predator mortality</td>
<td>0.8</td>
<td>C. Walters pers. comm. 2000</td>
</tr>
<tr>
<td>v1</td>
<td>Flow of invulnerable prey pool into vulnerable prey pool</td>
<td>30</td>
<td>Trial &amp; error; (Hodges et al 2001)</td>
</tr>
<tr>
<td>v2</td>
<td>Flow of vulnerable prey pool into invulnerable prey pool</td>
<td>1</td>
<td>Set relative to v1</td>
</tr>
</tbody>
</table>
Figure 2.1: Schematic of continuous predator prey model with harvesting applied. A large number of prey (v1) move from the invulnerable prey pool to foraging and mating areas where they are vulnerable to predators or hunters; a much smaller number move back to the invulnerable prey pool (v2).
Figure 2.2: Prey and predator abundance from a. the without harvesting model, b. the with harvesting model, and c. prey density under both harvest regimes.
Figure 2.3: The fit of the predicted data to the observed snowshoe hare harvest data for Newfoundland, 1966-1999.
Figure 2.4: The predicted proportion of snowshoe hares harvested in Newfoundland derived by fitting the predator-prey model to the observed harvest data.
Figure 2.5: The relationship between the proportion of vulnerable prey (Vn) harvested and the length of the low predicted by the model. The dots represent the data the dashed line is the second order polynomial trendline.
Figure 2.6: The changes in the prey and predator per hectare resulting from varying each parameter individually from the values used in the model (see Table 2.1). The thick line is the prey per hectare, thin line the predators per hectare.
Chapter 3

Hunting impacts on snowshoe hare population abundance:
Live-trapping

Introduction

Management policies for snowshoe hare harvesting have been governed by the fact hares have a high fecundity rate (Hodges 1999), and the assumption that populations are relatively unaffected by hunting (Gilbert and Dodds 1992). As a result, we lack basic harvest management strategies for the snowshoe hare, the keystone species of the boreal forest ecosystem.

In Newfoundland, the hunting season for snowshoe hares runs from early October to late February, a period of non-breeding for hares. Historically, Newfoundlanders harvested an average 1,000,000 hares each year (Figure 1.3). Removal of hares during the non-breeding season is expected to cause a decrease in population density, unless immigration to the area or a decrease in natural mortality or emigration compensates for the loss (Figure 1.1).

Long-term effects of hunting on snowshoe hare populations are possible. Hunting may decrease the spring breeding population simply by removing potential breeders, thereby reducing the probability of recovery of losses through recruitment. In addition following the theory of adaptive antipredator behavior (Abrams 1993, Hik 1995), hares may react to hunters through a reduction in movement and foraging, thereby lowering the condition of survivors, in particularly females, which could lead to lower fecundity. Decrease in the number of breeders or female fecundity may result in slower growth of a
hunted population and its predators. For a cyclic snowshoe hare population, such may produce a longer cycle then would otherwise be seen as was suggested by the model in Chapter 2.

Removal studies in the Yukon by Boutin (1980) and in British Colombia by Sullivan and Sullivan (1986) indicated that colonization of areas with reduced densities by snowshoe hares is variable. The amount of immigration appears to be influenced by the amount of the reduction and the size of the area involved. Research into snowshoe hare movement and home ranges argue that although hares can move long distances, generally they do not (Broche 1975, Wolff 1980, Keith et al 1993, Hodges 1998, Gillis and Krebs 1999). Therefore, the probability that they would move into the interior of large removal areas is low.

The purpose of this study is to examine the effects of harvesting on snowshoe hare populations in Newfoundland during a cyclic peak. I predicted that 1) there would be a negative impact of hunting on local population sizes within a hunting season; 2) there would be lower recruitment into the fall population of the next year on the hunted sites compared to the control sites; and 3) hares on the hunted sites would be in poorer condition due to antipredator behavior, particularly where dogs are used for hunting.

Methods

I set up two pairs of hunted and control grids, each 25 ha in size, to mark and recapture snowshoe hares before, during and after the five-month hunting season in Newfoundland. One pair of these grids was on the Avalon Peninsula and the other was about 250 km to the west, on the eastern coast of the island (Figure 1.1).
**Study areas**

*Butter Pot Provincial Park and MUN Woodlot*

Butter Pot Provincial Park and MUN Woodlot are found in the Northeast Maritime Barrens Subregion of the Avalon Peninsula in eastern Newfoundland as defined by Meades and Moores (1989; Figure 1.1). Despite its name, this area is heavily forested with balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*) and peppered with small wetlands, *Kalmia* heaths and lichen barrens. The edges of these breaks in the forest are favorite hunting areas for hunters using dogs to force the snowshoe hares into the open. Small mature white birch (*Betula papryrifera*) stands exist within both trapping grids with little regeneration. This area experiences frequent fog and strong winds, resulting in the coldest summers for Newfoundland. The normal summer temperatures are typically in the low to mid 20°C’s. The winters are relatively mild with regular thaws and winter rain limiting snow accumulation. For the MUN Woodlot, hunters used dog(s) and rifle to harvest hares.

*Terra Nova National Park and Port Blandford Woodlot*

Terra Nova National Park (TNNP) and Port Blandford Woodlot are located on the east coast of Newfoundland (Figure 1.1) within the Northcentral Subregion, as defined by Meades and Moores (1989). The area consists of various vegetation regimes, the main ones being forest, softwood scrub and wetlands. The forested areas are dominated by black spruce with white spruce (*Picea glauca*), balsam fir and hardwoods. Hardwoods include white birch and trembling aspen (*Populus tremuloides*). For TNNP, domestic and commercial logging ceased in 1957 with the establishment of the park. The trapping grid in TNNP is located at the southern end of the park at Dunphy’s Pond. The
Northcentral Subregion is classified as having higher summer temperatures high 20°C's to low 30°C's and low rainfall; winters are cold, with snow generally lasting through the winter, although accumulations are low, <3 m. Snares are the main hunting method used in Port Blandford, however during highs in the hare population a rifle may also be used to take hares flushed while checking snares.

Trapping grid

We selected the sites of our trapping grids between November 1998 and July 1999 using several criteria. The first restriction on the grid site location was accessibility. The areas had to be less than a 30-minute walk from a road accessible by a truck, to minimize the amount of time the snowshoe hares remained in the cages. For the hunted areas, accessibility was also necessary to ensure sufficient hunting was occurring in the area. All grids were placed along existing trails to provide access by field staff and to ensure that the park grids experienced human activity year-round, as occurred on the hunted grids. The level of such activity was higher in the hunted areas though, because walkers and skiers using the park grids generally stayed on the trails, while hunters did not.

Grid sites were initially selected using colored aerial photographs and discussions with the local Wildlife Conservation Officers. Potential areas were walked through to determine suitability of the sites. Control areas (parks) were selected first, as these were the most difficult to find, and then hunted areas that matched them in habitat composition were identified. Within the park areas, it was necessary to select grid sites that were a minimum of 1 km away from hunted areas, to reduce the risk of snowshoe hares within
the grids moving to voids created by hunting at park boundaries. Attempts were made to locate a third control site, but the two parks selected were the only non-hunted areas of suitable size and configuration on the island of Newfoundland that did not require a helicopter to access. Terra Nova National Park was of sufficient size for a second grid, but all other areas of suitable habitat were inaccessible.

The hunted areas were experimental woodlots set aside by the provincial Forestry Division to monitor the natural progression of a forested area without the disturbance of logging or silviculture activities. Selection of such areas was necessary to match the age structure and natural disturbance regime of the study areas within the parks. As well, it was necessary to ensure that logging did not occur during the course of the study, which is scheduled to continue through the next snowshoe hare population decline. Areas near communities were selected as such areas sustained high hunting pressure due to the proximity to towns. The level of hunting activity was initially determined by discussing various locations with the local Wildlife Conservation Officers. Hunting was confirmed by the regular presence of hunters or snares. The hunted grids were placed inside larger hunted areas, to reduce the likelihood of immigration of hares from adjacent non-hunted areas.

The trapping grids, each measuring 500 x 500 m, were set up using a 2-km string box or hip chain and compass. Grid borders were verified at the end of each line by back checking to the previous line, and adjustments were made where necessary. I systematically placed 50 Tomahawk traps (Tomahawk Live trap Company, Tomahawk, WI) within each site on a 14 x 14 station grid, with traps 77 m apart.
Trapping protocol

Trapping began in January 1999 on the Butter Pot Provincial Park and MUN Woodlot grids to gather initial data, test study protocols, train assistants, and monitor hunter interference with cages in the woodlot. During March 1999, a second pair of grids was established 250 km west of the first pair in Terra Nova National Park and Gambo Woodlot. Trapping began in April of that year. The Gambo Woodlot proved to be problematic, with black bears frequently destroying cages and killing snowshoe hares; all attempts to remove the bears were unsuccessful. In addition, illegal logging began on and near the grid. Therefore, in July 1999, a second grid, Port Blandford Woodlot, was established in a hunted area 20 km outside Terra Nova National Park. Trapping began on this site in August 1999. Trapping on the Gambo grid occurred sporadically between September 1999 and April 2000, after which the grid was disassembled. For the 1999-2000 field season, trapping began between late September after the Parks closed to campers and early October before the hunting season opened, and continued at least one month after the close of hunting season at the end of February.

I also planned to trap our grids during a second season, from November 2000 to April 2001, but this did not occur due to the heavy snowfall. Following 27 days of rain in November, 13 m of snow fell on the east coast of Newfoundland between December and April. There was 3 m of snow accumulated on the grids by late December, and they were not free of snow until mid-June. There was no sign of hunting on any of the grids after December. I was able to conduct the before-hunting trapping session in late September to early October 2001, as planned.
My trapping protocol was driven by two assumptions of mark-recapture statistics. The first is that survival of marked and unmarked individuals is the same. Negative effects of trapping and marking would result in an overestimate of snowshoe hare abundance. Work from Kluane Boreal Ecosystem Project showed that survival rates were lower for snowshoe hares that had been captured every 2–3 weeks compared to populations trapped only twice per year (Hodges et al 2001). To reduce the impact on survival, I scheduled trapping sessions at least five weeks apart. I trapped for two days, and then stopped for a day or two before resuming for another day or two (Hodges et al 2001). Trapping did not occur if the weather forecast called for rain, more than 5 cm of snow, or temperatures below −15°C. Second, the population being trapped had to be closed to substantial mortality or immigration, particularly losses that were not consistent between the grids being compared. Therefore, on the hunted grids, it was necessary to complete trapping within one week from Saturday night to Friday morning, as the majority of hunting occurred on Saturday. When the one-week limit was combined with the restriction on repeated trapping stated above, four nights per grid was the maximum possible per session, and I often only trapped for 3 nights if the weather was unsuitable. This limited the trapping on the control grids as well, because the grids were trapped as pairs and although they may not have been set on the same day, trapping occurred within the same week.

On the first capture, snowshoe hares greater than 700g were ear-tagged with numbered tags (Montel No 3 tag, series A0001-1999, National Band and Tag Company, Newport, KY). For every capture, I recorded trap location, weight (g), eartag number, presence of ticks (0–2, where 0 = none, 1 = few, 2 = many), right hind foot length (mm),
sex, percent white, and injuries. Snowshoe hares were checked for lactation or scrotum position.

Data analysis

I calculated population abundances to detect differences due to hunting. For each grid and trapping session, population abundance was estimated using the Jackknife procedure in CAPTURE® software (Otis et al 1978, White et al 1982). The use of the Jackknife estimator was recommended by Boulanger and Krebs (1994) in a comparison of Jolly-Seber estimates and estimates from 7 models of CAPTURE. They found the Jackknife estimator, which models capture probability for individual heterogeneity, to be robust and the least biased. They also suggest that, when making comparisons, it was best to use the same estimator for all calculations.

Immigration was calculated as the number and percent of hares caught on the grid for the first time during each trapping session. As natural mortality was not assessed, it was not possible to separate emigration from mortality. Emigration plus mortality was calculated as the number of hares caught only once (Hodges et al. 2001). For this calculation, the last trapping sessions were excluded from the calculations as the hares caught only once for these dates were first time captures and had no chance of recapture.

Differences between control and hunted grids for the proportion of hares caught for the first time and the proportion caught only once was tested using two sample t-tests (Systat 10, SPSS Inc. 2000). Statistical significance was determined at $\alpha = 0.05$ and the power ($\beta$) of the t-test to detect differences between the samples was calculated for tests with $p > 0.05$ (Thomas and Juanes 1996).
Snowshoe hare weights taken during trapping were analyzed for differences between the hunted and control grids.

The 25 hectares covered by each grid represents the minimum area occupied by the population of hares. The actual area inhabited by all trapped hares on a grid is larger, due to the trapping of hares that live at the outside edge of the grid. I used the straight-line distance between consecutive captures as a measure of the extent of movement by the hares. The mean of the distances between captures for all grids determined the effective trapping area of the grids, the mean distance was added to each side of the minimum grid.

**Results**

There were 521 snowshoe hares tagged in this study with a total of 2286 captures (Table 3.1). Population abundances on both control grids remained stable throughout the trapping season while substantial declines were seen in both hunted areas (Figure 3.1). The main trapping session began on both pairs of grids in September 1999 with the pre-hunt survey. Pre-hunt population estimates were similar for all grids (Figure 3.1, Table 3.2). By January 2000, a substantial drop had occurred in the populations on the hunted grids; the January populations were 46% and 77% of the fall populations on the MUN Woodlot and Port Blandford, respectively, compared to 91% for Butter Pot Park and 98% for TNNP. Two sample t-test on the proportion of change in population estimates from September to January indicate that there is no difference between the control and hunted grids ($t = 2.125$, $df = 2$, $p = 0.168$). However, with the small sample size available here
the power of the test is low, \( \beta = 0.370 \) and using the means and standard deviations from the above test a sample size of 5 is required for \( \beta = 0.95 \).

On the MUN Woodlot grid, a large increase in population estimates for 1999 and 2000 was seen at the end of each hunting season 20% and 28%, respectively (January compared to March; Figure 3.2a). This change was not reflected in the control area Butter Pot Park, which actually experienced a decrease in the population estimates for both years, -8% and -7%, respectively. The TNNP and Port Blandford grids both experienced smaller increases in the population estimates over this time period, 11% and 3%, respectively. Comparing the proportion of change in population estimates from January to March for control and hunted grids using a t-test found no difference (\( t = -1.97, \text{df} = 4, p = 0.120 \)). For this test, the power was low at \( \beta = 0.386 \), and using the means and standard deviations from the above test a sample size of 9 is required for \( \beta = 0.95 \).

Changes from spring (March) to fall (September) population estimates for 1999 and 2000 (Figure 3.2b) indicated higher growth for snowshoe hare populations on the hunted grids (50% to 96% growth) as compared to the control grids (-16% to 26%; \( t = -3.38, \text{df} = 4, p = 0.020 \)).

Immigration of snowshoe hares did not differ between the control and hunted areas (Figure 3.3). The mean number of new hares tagged excluding January 1999 for Butter Pot Park and MUN Woodlot and September 1999 for TNNP and Port Blandford were 31%, 35%, 48% and 27%, respectively. Emigration plus mortality showed no discernable pattern (Figure 3.4) with mean of 15% for Butter Pot Park, 10% for MUN Woodlot, 12% for TNNP, and 8% for Port Blandford.
The mean straight line distance between consecutive locations was 86.6 m. If this was used as the radius of a circular home range, the area would be about 4.5 ha. When applied to the edge of the 25-ha trapping grid, the resulting effective trapping area was 45 ha. The snowshoe densities for all sites based on the effective trapping grid size ranged from 0.56 to 1.78 hares per ha (Table 3.2a-d).

Snowshoe hare populations on all grids experienced a significant decrease from September 2000 to September 2001 (Figure 3.2, t = 6.194, df = 3, p = 0.009). Percent changes in population estimates ranged from −28% to −59% with no difference between hunted and control areas (Table 3.3).

Weights did not differ between snowshoe hare trapped on control and hunted grids. The means were 1299.5g for the control grids and 1288.5g for the hunted (F = 1.567, df = 2057, p = 0.211).

Discussion

I observed declines in population abundances on both hunted grids, while the abundance of snowshoe hares on control grids remained stable throughout the hunting season, as was expected. Hunting losses during a non-breeding season may be compensated for by increased immigration or reduced emigration plus mortality (Figure 1.1). In this study from September to March, immigration to the hunted grids during each trapping session were similar to that onto the control grids, and therefore did not compensate for hunting losses. Furthermore, emigration plus mortality did not differ between control and hunted grids.
These results were similar to a removal study by Boutin (1980). In this Yukon study, 10 of 22 radio-collared females with known home ranges were removed during breeding season to create a large area vacant of female hares by (Boutin 1980). The number of immigrants (males and females) into the removal area was similar to that on a control site. In addition, the remaining collared females did not move into the removal area although they did increase the amount of time spent at the edges of their home ranges closest to it.

In contrast, a second removal study in northern British Colombia reported large-scale movement to a removal site (Sullivan and Sullivan 1986). This study attempted to remove all snowshoe hares from a 9-ha grid over a 2-year period to prevent overbrowsing of lodgepole pine seedlings during a cyclic high. The recovery of hare numbers on the removal area ranged from 58% to 215% during each 4-week period, showing a great capacity for hares to re-colonize the site. The rate of immigration to the removal grid was 156% higher than on the control grid. The relatively small grid size utilized by Sullivan and Sullivan (1986) compared to home range size of a snowshoe hare (5 to 10 ha, Hodges 1999) may explain the high re-colonization they observed.

The disagreement in results between Boutin (1980) and Sullivan and Sullivan (1986) may be to some degree a seasonal effect. Sullivan and Sullivan (1986) reported that movement of snowshoe hares into the removal area was highest in winter and autumn and lowest in spring and early summer. The reduced movement during the summer may explain the lack of movement into the removal site observed by Boutin. This was also supported by Windberg and Keith (1976), who reported that female snowshoe hares in Alberta did not shift their home ranges during breeding although they
were more mobile during peak years. However, Hodges (1998) found overall summer movement rates to be higher relative to winter rates, possibly due to the cold winter temperatures of the Yukon.

Neither of the removal studies by Boutin (1980) and Sullivan and Sullivan (1986) may be appropriate for predicting the effects of the removal of snowshoe hares by hunters. First, both studies experimented with areas much smaller than those typically covered by hunters. In this study, hunting occurred over an area of more than 75 ha. Reported home range sizes and movement rates also suggest that movement into the hunter removal areas would be low. Snowshoe hares are capable of traveling great distances. Results from telemetry studies indicate that snowshoe hares may move up to 500 m from their areas of regular use for brief periods, and they have been recorded traveling up to 20km (Keith et al 1993, Gillis 1998, Hodges 1998). Despite this ability, overall movement of hares was typically low and snowshoe hares generally intensively utilize small portions of their 5–10 ha home ranges, (ie. <3 ha; Wolff 1980, Hodges 1998, Hodges 1999). Similarly, Brocke (1975) reported that the greatest distances between locations for individual animals range from 210 to 462 m, based on telemetry data, and from 172 to 200 m using trapping data. Therefore, it may not be realistic to expect large-scale immigration into larger heavily-hunted areas.

Second, the intensity of the removal in the small study areas was greater. Hunting with snares or dogs and rifle is not as successful as live-trapping (T. Joyce unpubl. observation). In general, over a small area, hunting would remove fewer animals than live trapping, but hunters remove animals over a much greater area. Therefore, hunting will reduce the overall density of a large area through a partial removal similar to
Boutin’s experiment, rather than creating small voids as was done by Sullivan and Sullivan (1986).

Mortality of hares from hunting may be at least partly compensated by reduced natural mortality. In areas without hunting, predation, the main cause of natural mortality, accounts for >90% of the deaths, and annual survival can range from 32% during the cyclic increase to <1% during a population decline (Hodges 2001). In a study of the effects of hunting mortality on brown hare populations in France, Pielowski (cited in Pepin 1987) reported a decrease of >50% in natural mortality when hunting increased from 25% to 40% of the fall population. If natural mortality compensated for the hunting loss, then I should not have seen a difference between the hunted and control grids as the hunting season progressed. Even though I did not measure hunting mortality levels the hunted populations did decline more rapidly then those on the control sites in this study, and therefore a total reduction in natural mortality to compensate for hunting loss did not occur.

Despite the declining populations recorded on the hunted grids during hunting season, the expected lower recruitment on these grids was not observed. In fact, the increase in populations from the start of breeding in March to the following September was higher for the hunted areas, indicating that, at least during a cyclic high, hare populations can recover from hunting impacts. The mechanism of this recovery, however, is not known. It may be an increase in reproductive output by females on the hunted grids, although such would be unlikely unless reproduction was limited on the control grids. The snowshoe hare population in Butter Pot Park did show a slight decline in September 2000 compared to September 1999. And in light of the sharp decline
observed in September 2001, the Butter Pot Park hare population in September 2000 may have been limited. However, this was not seen on the other control grid. The second mechanism of input into a population is immigration (Figure 1.1). However, higher immigration into the hunted grid compared to the control grid would be contradictory to the results that there is no difference in immigration. Other possible mechanisms would be reduced output from the population during the summer. Animals leave a population through natural mortality and emigration (Figure 1.1). Therefore, natural mortality may be lower, possibly due to fewer predators on the hunted grids in response to competition with hunters, or emigration is lower. Lower emigration on the hunted grid compared to the control grid is contradictory to our results of no difference.

Survey results from September 2001 indicated that there is a widespread decline in snowshoe hare populations of eastern Newfoundland. This finding is consistent with the increase in lynx sightings reported during the summer months (see Chapter 1) which generally corresponds with a reduction in the prey base for the lynx (M. O’Donoghue pers. comm. 2001).

Snowshoe hares do not appear to be greatly affected by human presence. They are often sighted within communities and feeding on neighborhood ornamental gardens. When encountered in the wilderness they may only move a short distance away. However, hunting can greatly increase the number of human encounters which may be particularly stressful to hares when dogs are included. Abrams (1993) proposed, under adaptive anti-predator behavior, that prey will reduce movement to avoid predators when predators are at high densities. I suggested that such behavior may result in less foraging and lower weights for snowshoe hares on the hunted grids compared to the control grids.
particularly on the MUN Woodlot grid, where dogs were used for hunting. This was not observed, weights did not differ between control and hunted grids. However on the MUN Woodlot grid, there was a large increase (>20%) in population estimates for the March, post-hunting sessions in 1999 and 2000 compared to the January estimates. This increase may be, in part, attributed to an increase in movement by snowshoe hares due to the absence of hunters and dogs, thereby giving support to adaptive antipredator behavior.

In conclusion, declines in population abundances on both hunted grids were observed, while the abundance of snowshoe hares on control grids remained stable. The effect was not long term. Despite the declines on the hunted grids as least during this period of high snowshoe numbers, populations recover from hunting impacts. The mechanism of recovery was not explored in this study, but is expected to be related to decreased natural mortality. On the MUN Woodlot grid where dogs were used for hunting, there was more than a 20% increase in estimated population sizes for 1999 and 2000 following the end of hunting season. This increase was not seen on the control grids or on the grid hunted with snares, giving support to the theory of adaptive antipredator behavior. Population estimates for September 2001 indicate snowshoe hare populations in Newfoundland are entering the declining phase of the cycle.

Summary

I monitored changes to snowshoe hare abundances on two control (non-hunted) and two hunted grids within a hunting season with mark-recapture techniques. Live-trapping began in September 1 month prior to hunting season opening, and continued
through the hunting season to March 1 month post hunting season. Population estimates were calculated using Jackknife estimator in CAPTURE software. Substantial declines were seen in both hunted areas, 46% and 77% of the fall populations, while the control areas remained stable at 91% and 98%. There was some recovery in the population following the end of harvesting on the grid hunted with dogs that was unlikely to be due to immigration. This recovery supported Abrams's (1993) theory of adaptive antipredator behavior, which centres on a reduction in movement by a prey species when predators are abundant. Both hunted populations recovered from harvesting by the following fall probably through a combination of summer recruitment and natal dispersal. Declines in population estimates of September 2001 compared to September 2000 indicated that the population was entering a cyclic decline. There was no difference in the timing of declines between the control and the hunted grids.
Table 3.1: The number of individual hares captured and the number of total captures for each grid for January 1999 to September 2001. Butter Pot Park and Terra Nova National Park (TNNP) were the control grids, and MUN and Port Blandford Woodlots were hunted grids.

<table>
<thead>
<tr>
<th>Grids</th>
<th>Number of individual hares tagged</th>
<th>Number of recaptures</th>
<th>Total number of captures</th>
</tr>
</thead>
<tbody>
<tr>
<td>Butter Pot Park</td>
<td>120</td>
<td>382</td>
<td>502</td>
</tr>
<tr>
<td>MUN Woodlot</td>
<td>132</td>
<td>368</td>
<td>500</td>
</tr>
<tr>
<td>TNNP</td>
<td>139</td>
<td>571</td>
<td>710</td>
</tr>
<tr>
<td>Port Blandford Woodlot</td>
<td>130</td>
<td>444</td>
<td>574</td>
</tr>
<tr>
<td>TOTAL</td>
<td>521</td>
<td>1765</td>
<td>2286</td>
</tr>
</tbody>
</table>
Table 3.2a: Jackknife population estimator statistics from CAPTURE for Butter Pot Provincial Park grid. The trapping grid is 25ha and effective trapping grid is 45ha.

Hunting season status is indicated as pre-hunt, hunt and post-hunt.

<table>
<thead>
<tr>
<th>Date</th>
<th>Average probability of capture p-hat</th>
<th>Trapping nights</th>
<th>Number of individuals captured</th>
<th>Population estimate (95% CI)</th>
<th>Co-efficient of variation (% of N)</th>
<th>Effective trapping grid density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan 1999 (Hunt)</td>
<td>0.366</td>
<td>3</td>
<td>41</td>
<td>61 (52-78)</td>
<td>6.70 (11.0)</td>
<td>1.36</td>
</tr>
<tr>
<td>Mar 1999 (post)</td>
<td>0.429</td>
<td>3</td>
<td>42</td>
<td>56 (49-72)</td>
<td>5.74 (9.76)</td>
<td>1.24</td>
</tr>
<tr>
<td>Apr 1999 (post)</td>
<td>0.603</td>
<td>3</td>
<td>46</td>
<td>52 (48-64)</td>
<td>3.71 (7.1)</td>
<td>1.16</td>
</tr>
<tr>
<td>Sep 1999 (pre)</td>
<td>0.426</td>
<td>3</td>
<td>34</td>
<td>47 (40-62)</td>
<td>5.47 (11.6)</td>
<td>1.04</td>
</tr>
<tr>
<td>Nov 1999 (Hunt)</td>
<td>0.333</td>
<td>3</td>
<td>32</td>
<td>48 (40-64)</td>
<td>6.08 (12.7)</td>
<td>1.07</td>
</tr>
<tr>
<td>Jan 2000 (Hunt)</td>
<td>0.333</td>
<td>3</td>
<td>29</td>
<td>43 (36-59)</td>
<td>5.70 (11.8)</td>
<td>0.96</td>
</tr>
<tr>
<td>Mar 2000 (post)</td>
<td>0.421</td>
<td>3</td>
<td>28</td>
<td>40 (35-57)</td>
<td>4.72 (11.8)</td>
<td>0.89</td>
</tr>
<tr>
<td>Sep 2000 (pre)</td>
<td>0.472</td>
<td>4</td>
<td>37</td>
<td>44 (40-57)</td>
<td>4.09 (3.9)</td>
<td>0.98</td>
</tr>
<tr>
<td>Sep 2001 (pre)</td>
<td>0.426</td>
<td>3</td>
<td>14</td>
<td>18 (16-29)</td>
<td>3.11 (17.7)</td>
<td>0.40</td>
</tr>
</tbody>
</table>
Table 3.2b: Jackknife population estimator statistics from CAPTURE for MUN Woodlot hunted grid. The trapping grid is 25ha and effective trapping grid is 45ha. Hunting season status is indicated as pre-hunt, hunt and post-hunt.

<table>
<thead>
<tr>
<th>Date (season status)</th>
<th>Average probability of capture $p$-hat</th>
<th>Trapping nights</th>
<th>Number of individuals captured</th>
<th>Population estimate (95% CI)</th>
<th>Co-efficient of variation (% of N)</th>
<th>Effective trapping grid density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan 1999 (Hunt)</td>
<td>0.411</td>
<td>3</td>
<td>22</td>
<td>30 (25-43)</td>
<td>4.31 (14.4)</td>
<td>0.67</td>
</tr>
<tr>
<td>Mar 1999 (post)</td>
<td>0.528</td>
<td>3</td>
<td>30</td>
<td>36 (33-48)</td>
<td>3.80 (10.5)</td>
<td>0.80</td>
</tr>
<tr>
<td>Apr 1999 (post)</td>
<td>0.719</td>
<td>3</td>
<td>30</td>
<td>32 (31-44)</td>
<td>2.62 (8.2)</td>
<td>0.71</td>
</tr>
<tr>
<td>Sep 1999 (pre)</td>
<td>0.315</td>
<td>3</td>
<td>35</td>
<td>54 (45-71)</td>
<td>6.55 (12.3)</td>
<td>1.20</td>
</tr>
<tr>
<td>Nov 1999 (Hunt)</td>
<td>0.383</td>
<td>3</td>
<td>28</td>
<td>40 (34-55)</td>
<td>5.35 (13.4)</td>
<td>0.89</td>
</tr>
<tr>
<td>Jan 2000 (Hunt)</td>
<td>0.507</td>
<td>3</td>
<td>21</td>
<td>25 (22-36)</td>
<td>3.07 (12.3)</td>
<td>0.56</td>
</tr>
<tr>
<td>Mar 2000 (post)</td>
<td>0.500</td>
<td>3</td>
<td>26</td>
<td>32 (28-43)</td>
<td>3.59 (11.2)</td>
<td>0.71</td>
</tr>
<tr>
<td>Sep 2000 (pre)</td>
<td>0.349</td>
<td>4</td>
<td>44</td>
<td>63 (53-83)</td>
<td>7.48 (11.9)</td>
<td>1.40</td>
</tr>
<tr>
<td>Sep 2001 (pre)</td>
<td>0.317</td>
<td>3</td>
<td>29</td>
<td>40 (34-55)</td>
<td>5.21 (13.0)</td>
<td>0.89</td>
</tr>
</tbody>
</table>
Table 3.2c: Jackknife population estimator statistics from CAPTURE for Terra Nova National Park grid. The trapping grid is 25ha and effective trapping grid is 45ha. Hunting season status is indicated as pre-hunt, hunt and post-hunt.

<table>
<thead>
<tr>
<th>Date</th>
<th>Average p-hat</th>
<th>Trapping nights</th>
<th>Number of individuals captured</th>
<th>Population estimate (95% CI)</th>
<th>Co-efficient of variation (% of N)</th>
<th>Effective trapping grid density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sep 1999 (pre)</td>
<td>0.233</td>
<td>4</td>
<td>33</td>
<td>58 (47-81)</td>
<td>8.66 (14.9)</td>
<td>1.29</td>
</tr>
<tr>
<td>Nov 1999 (Hunt)</td>
<td>0.449</td>
<td>4</td>
<td>44</td>
<td>54 (48-68)</td>
<td>4.77 (8.8)</td>
<td>1.20</td>
</tr>
<tr>
<td>Jan 2000 (Hunt)</td>
<td>0.468</td>
<td>3</td>
<td>44</td>
<td>57 (50-72)</td>
<td>5.46 (9.6)</td>
<td>1.27</td>
</tr>
<tr>
<td>Feb 2000 (Hunt)</td>
<td>0.440</td>
<td>4</td>
<td>47</td>
<td>58 (52-73)</td>
<td>5.14 (8.9)</td>
<td>1.29</td>
</tr>
<tr>
<td>Mar 2000 (post)</td>
<td>0.524</td>
<td>3</td>
<td>50</td>
<td>63 (56-79)</td>
<td>5.56 (8.8)</td>
<td>1.40</td>
</tr>
<tr>
<td>Sep 2000 (pre)</td>
<td>0.309</td>
<td>4</td>
<td>54</td>
<td>80 (68-104)</td>
<td>8.99 (11.2)</td>
<td>1.78</td>
</tr>
<tr>
<td>Dec 2000 (Hunt)</td>
<td>0.386</td>
<td>3</td>
<td>49</td>
<td>70 (60-88)</td>
<td>6.97 (10.0)</td>
<td>1.56</td>
</tr>
<tr>
<td>Sep 2001 (pre)</td>
<td>0.341</td>
<td>3</td>
<td>29</td>
<td>43 (36-59)</td>
<td>5.74 (13.3)</td>
<td>0.96</td>
</tr>
</tbody>
</table>
Table 3.2d: Jackknife population estimator statistics from CAPTURE for Port Blandford hunted grid. The trapping grid is 25ha and effective trapping grid is 45ha. Hunting season status is indicated as pre-hunt, hunt and post-hunt.

<table>
<thead>
<tr>
<th>Date</th>
<th>Average probability of capture of individuals captured</th>
<th>Trapping probability nights</th>
<th>Number of individuals captured</th>
<th>Population estimate (95% CI)</th>
<th>Co-efficient of variation (% of N)</th>
<th>Effective trapping grid density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sep 1999 (pre)</td>
<td>0.442</td>
<td>4</td>
<td>32</td>
<td>39 (35-53)</td>
<td>4.36 (11.2)</td>
<td>0.87</td>
</tr>
<tr>
<td>Nov 1999 (Hunt)</td>
<td>0.403</td>
<td>4</td>
<td>37</td>
<td>54 (45-74)</td>
<td>7.11 (13.2)</td>
<td>1.20</td>
</tr>
<tr>
<td>Jan 2000 (Hunt)</td>
<td>0.467</td>
<td>3</td>
<td>24</td>
<td>30 (26-41)</td>
<td>3.59 (12.0)</td>
<td>0.67</td>
</tr>
<tr>
<td>Feb 2000 (Hunt)</td>
<td>0.540</td>
<td>4</td>
<td>23</td>
<td>25 (24-38)</td>
<td>2.88 (11.5)</td>
<td>0.56</td>
</tr>
<tr>
<td>Mar 2000 (post)</td>
<td>0.720</td>
<td>3</td>
<td>30</td>
<td>31 (31-44)</td>
<td>2.39 (7.7)</td>
<td>0.69</td>
</tr>
<tr>
<td>Sep 2000 (pre)</td>
<td>0.378</td>
<td>3</td>
<td>42</td>
<td>60 (51-77)</td>
<td>6.53 (10.9)</td>
<td>1.33</td>
</tr>
<tr>
<td>Dec 2000 (Hunt)</td>
<td>0.471</td>
<td>3</td>
<td>36</td>
<td>46 (41-60)</td>
<td>4.88 (10.6)</td>
<td>1.02</td>
</tr>
<tr>
<td>Sep 2001 (pre)</td>
<td>0.581</td>
<td>3</td>
<td>36</td>
<td>43 (39-55)</td>
<td>3.91 (9.09)</td>
<td>0.96</td>
</tr>
</tbody>
</table>
Table 3.3: Percent change in population estimates from Sept 1999 to Sept 2000 and from September 2000 to 2001 population survey results.

<table>
<thead>
<tr>
<th>Grid</th>
<th>Percent change in population estimates from Sept 1999 to Sept 2000</th>
<th>Percent change in population estimates from Sept 2000 to Sept 2001</th>
</tr>
</thead>
<tbody>
<tr>
<td>Butter Pot Park (control)</td>
<td>-6.4</td>
<td>-59.1</td>
</tr>
<tr>
<td>MUN Woodlot (hunted)</td>
<td>16.7</td>
<td>-36.5</td>
</tr>
<tr>
<td>TNNP (control)</td>
<td>37.9</td>
<td>-38.6</td>
</tr>
<tr>
<td>Port Blandford (hunted)</td>
<td>53.8</td>
<td>-28.3</td>
</tr>
<tr>
<td>Mean</td>
<td>25.5</td>
<td>-40.6</td>
</tr>
</tbody>
</table>
Figure 3.1: Results of live trapping snowshoe hares before (September), during (October-February) and after (March, April) hunting season on two pairs of grids (hunted and control). Population estimates (± 95% C.I.) were calculated using the Jackknife estimator in CAPTURE computer software.
Figure 3.2: Fall population survey results for each of the trapping grids in eastern Newfoundland, 1999-2001. Population estimates (± 95% C.I.) were calculated using the Jackknife estimator in CAPTURE computer software. The hunting season starts in October.
a. January to March

b. March to September

Figure 3.3: Percent change in population estimates for the control (shaded bars) and hunted (white bars) grids for (a). January to March and (b). March to September. TNNP and Port Blandford Woodlot pair only has data for 2000.
Figure 3.4: The number of new snowshoe hares tagged during each trapping session as measure of immigration to the grid. Trapping did not occurred during February 2000 on the Butter Pot Park and MUN Woodlot grid.
Figure 3.5: The number of snowshoe hares caught in only one trapping session as a measure of emigration and mortality on control and hunted grids.
Figure 3.6: Mean weights (g) of snowshoe hares trapped during each trapping session on control and hunted grids. Note the y-axis starts at 1150g.
Chapter 4

Counting snowshoe hare pellets: plot shape, pellet degradation and an index of hunting effort.

Introduction

Population size estimates are a minimum requirement for effective management of hunted populations. However, costs associated with regular collection of data to estimate population size, on a species as widely distributed as the snowshoe hare, are prohibitive when live-trapping or radio-telemetry techniques have to be used. Pellet counts are seen as a cost-effective way to determine species abundance (Krebs et al 2001a).

The purpose of this chapter is to determine the most efficient pellet plot shape for the eastern Newfoundland forest, to assess the rate of pellet degradation, and to use pellet counts to examine the impact of hunting at a park boundary on abundance of hares. I suspected that in Newfoundland pellets degrade in less than 1 year, therefore pellet sampling may have to be more completed frequently. If hares are sedentary, hunting will influence hare numbers at the park edge so that more hares would be present inside the boundary than outside.

Methods

Pellet plot shape

In late April 1999, before leaf flush, I tested five different plot shapes, all approximately 1500 cm$^2$, 3 rectangular (5x300 cm, 10x150 cm, 15x100 cm), one square (38.7 x 38.7 cm) and one circular (radius = 21.9 cm). These shapes were tested over a range of habitat types within the Butter Pot grid, at least 2 m to the right of a trap stations (see Chapter 3). I avoided placing
the plots on established trails or next to trees that would fall within the plot. I carried out all pellet work to avoid sampler bias in including or excluding decaying pellets or those on the edges of the plots. Plots were not cleared previously, and so I developed criteria for which pellets I would count. Pellets that were firm (dark and light brown) and did not crumble were included. Vegetation was moved to view the ground level, but I did not disturb leaf litter or moss. Each plot size was tested at 20 stations. The order of shape testing was randomly selected for each station. A second person timed the counts with a stopwatch and recorded all information.

The index of cost for each plot was determined by multiplying the average time to search the plot by the variance of pellet counts for each plot shape. The lowest value indicated the optimal plot size (Krebs 1999, p. 111).

**Pellet degradation**

In January 1999, I collected 10 pellets each from under the cages of 15 snowshoe hares live-trapped in Butter Pot and placed them in a cluster to the side of the station in the most common vegetation types in the area to determine the rates of pellet degradation. The pellet clusters were marked with a stake, indicating date of collection and sample number. All cages had been cleared of any pellets when set the night before, so the collected pellets were all less than 24-hours old. The pellets were checked every two months from January to August 1999 and again before leaf flush in April 2000 (during December 1999, the markers were removed from 7 samples by field staff who had mistaken the pellet markers for cage markers, so only 8 were available for the final check). Snow cover over the pellets, when present, was not disturbed during this sampling. All clusters were counted and classified as moist or dry, dark or light.
brown, and firm or crumbling, based on the most common occurrence, such that if 6 pellets were dry and 4 moist, dry was recorded.

_Pellet transects for hunting index_

On the Butter Pot grid, I walked 3, 2-km transects with their midpoints at the park boundary, such that 1 km ran perpendicular to the boundary inside the park and 1 km perpendicular to the boundary outside the park. Using a string box or hip chain for measuring distance, I counted pellets within a 10x150 cm plot at 10m intervals along the transects as described above (Pellet plot shape section). The plots were not cleared or marked before sampling. An analysis of sample size using the variance from the plot shape exercise above indicated that a minimum sample of at least 84 plots was required. The 10 m frequency of counts resulted in 100 samples for each category, inside and outside the park.

I used two-sample Kolmogorov-Smirnov tests (Systat 10, SPSS Inc. 2000) with $\alpha = 0.05$ to assess differences in pellet abundance between plots inside and outside the park.

**Results**

_Pellet plot shape_

The testing of optimal plot shape took just over 2 hours to complete. The optimal plot shape was the 10x150 cm rectangle (Table 4.1).

_Pellet degradation_

Snow covered most samples from the end of February to late March and all pellets remained moist, dark brown and firm until after April 1999 (Table 4.2). By June, some decay
was noticeable, with pellets starting to dry and lightening in color, this continued to occur throughout the summer. Those clusters placed on moss (50% of collection) remained moist and dark longer than samples located on ground. All pellets remained firm, and no crumbling was observed. As the samples aged, some of the pellets began disappearing after 6 months (June 1999), particularly for the clusters located on moss. In August 1999, moss was gently searched under for the missing pellets with a large portion of the missing pellets being located. They were generally still moist and dark.

**Pellet transects for hunt index**

Pellet counts ranged from 0 to 11, with 45-55% of plots having 0 pellets (Appendix II). The two-sample Kolmogorov-Smirnov tests indicated no difference between the number of pellets counted inside and outside the park (Table 4.3).

**Discussion**

**Pellet plot shape**

Krebs et al (1987) found the rectangle 5x300 cm to be optimal for counting snowshoe hare pellets in the Yukon. Of those tested, the optimal plot shape for eastern Newfoundland is the rectangle 10x150 cm with the rectangle 5x300 cm taking longer and having higher variance in counts (Table 4.1). Eaton (1993) found a circle with radius of 1 m to be better than either rectangle 5x300 cm or rectangle 10x150 cm. These results support the recommendation by Krebs et al (2001a) that for different sites a variety of plot shapes and sizes should be assessed.
**Pellet degradation**

Within eight months, most collected pellets showed signs of decay in terms of being dry and lightening in color. The summer of 1999 was fairly wet and so four plots that rested on thick beds of moss retained relatively dark and somewhat moist hare pellets. The discovery of pellets beneath the moss identifies the care that must be taken in collecting pellet count data.

**Pellet transects**

There was no statistically significant difference between the number of pellets counted inside versus outside the park. It is possible that impacts of hunting on snowshoe hare numbers stretch into the non-hunted area beyond the 1 km tested here. However, the relatively short range of movement by hares makes this unlikely. The level of hunting for this area has not been estimated. Although dogs are used, hunting effort does not appear to be as intense as that on the MUN Woodlot grid, and it may not be sufficient to have a noticeable effect on the park population. Finally, during sampling the ground cover of each plot was not recorded. Therefore, it is not known how many plots occurred on moss and what affect this had on the counts.

In conclusion, I recommend that, where pellet plots are used, observers need to: 1) test plot shape and size for suitability to local ground cover conditions, with the caution that a standard plot should be used consistently where comparisons are to be made; 2) check the rate of pellet degradation to ensure sampling is completed at the appropriate interval; and 3) record ground cover type for each plot and monitor pellets for different rates of degradation.
Summary

Long-term monitoring of snowshoe hare abundances is needed. Fecal pellet counts provide an inexpensive mechanism for doing that. Care has to be taken in sampling design and sampling. A standard plot shape and size should be used where comparisons are going to be made. Initial testing of different plot shapes and sizes, over the range of ground cover conditions likely to be encounter, would determine the most efficient plot for those conditions. Pellet degradation should be monitored to ensure pellet counting is completed at the appropriate time interval. Ground cover should be thoroughly searched to avoid missing pellets.
Table 4.1. The results of testing 5 plot shapes for determining optimum quadrat shape for snowshoe hare pellet counts in Newfoundland. The index of cost was determined by multiplying the average time to cover the plot by the variance in pellets counts for that plot. These results were based on sampling of each shape 20 times. The area of all the shapes was approximately 1500 cm$^2$.

<table>
<thead>
<tr>
<th>Plot shape and dimensions</th>
<th>Average time (seconds)</th>
<th>Variance in pellet counts</th>
<th>Index of cost (time x counts)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rectangle: 5x300cm</td>
<td>53.1</td>
<td>1.69</td>
<td>89.7</td>
</tr>
<tr>
<td>Rectangle: 10x150cm</td>
<td>27.4</td>
<td>0.89</td>
<td>24.3</td>
</tr>
<tr>
<td>Rectangle: 15x100cm</td>
<td>19.9</td>
<td>1.49</td>
<td>29.7</td>
</tr>
<tr>
<td>Square (38.7 cm)$^2$</td>
<td>20.9</td>
<td>1.25</td>
<td>26.1</td>
</tr>
<tr>
<td>Circle (radius = 21.9 cm)</td>
<td>26.8</td>
<td>2.66</td>
<td>71.6</td>
</tr>
</tbody>
</table>
Table 4.2: The frequency of pellet groups in each degradation category checked from February 1999 to April 2000.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Moist, Dark, Firm</td>
<td>15</td>
<td>15</td>
<td>7</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Dry, Dark, Firm</td>
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<td>0</td>
<td>6</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Dry, Light, Firm</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>7</td>
<td>8</td>
</tr>
<tr>
<td>Crumbling</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>missing</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>7</td>
</tr>
</tbody>
</table>
Table 4.3: Mean, standard error (SE), standard deviation (SD) and Kolmogorov-Smirnov (KS) test results for pellets counted in 10x150 cm (1500 cm$^2$) plots inside and outside Butter Pot Park boundary.

<table>
<thead>
<tr>
<th>Transect</th>
<th>Location</th>
<th>N</th>
<th>Mean</th>
<th>SE</th>
<th>SD</th>
<th>KS</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>inside</td>
<td>100</td>
<td>1.15</td>
<td>0.186</td>
<td>1.861</td>
<td>0.030</td>
<td>p = 1.000</td>
</tr>
<tr>
<td></td>
<td>outside</td>
<td>100</td>
<td>0.980</td>
<td>0.150</td>
<td>1.504</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>inside</td>
<td>100</td>
<td>1.280</td>
<td>0.194</td>
<td>1.939</td>
<td>0.110</td>
<td>p = 0.581</td>
</tr>
<tr>
<td></td>
<td>outside</td>
<td>100</td>
<td>0.990</td>
<td>0.160</td>
<td>1.605</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>inside</td>
<td>100</td>
<td>0.780</td>
<td>1.150</td>
<td>1.000</td>
<td>0.080</td>
<td>p = 0.906</td>
</tr>
<tr>
<td></td>
<td>outside</td>
<td>100</td>
<td>0.900</td>
<td>0.163</td>
<td>1.150</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Chapter 5

Summary and Recommendations

Overview

Since snowshoe hares were introduction in the 1800s, they have featured prominently in the hunting culture of Newfoundland and has become the keystone species of its boreal forest. Despite the importance of the snowshoe hare, harvest management in Newfoundland has changed very little since it began 137 years ago. In fact, the lack of harvest management for snowshoe hares is a common thread across its North American range.

The purpose of this study was to assess the potential impact of harvesting on snowshoe hare populations in Newfoundland. The potential long-term effects of harvesting were examined through a modified Lotka-Volterra predator-prey model. The short-term effects were determined by monitoring snowshoe hare populations before, during and after hunting season in hunted and non-hunted areas. The main findings were:

1) Harvesting can reduce the abundance of hares during hunting season and this loss is not compensated by immigration.

2) At least during a cyclic high, snowshoe hare populations on hunted grids were able to recover by the next fall through a combination of recruitment and immigration, to levels comparable to control grids.

3) Adaptive antipredator behavior was supported by a large increase in the population hunted with dogs following the end of the hunting season. The increase was
not seen in the control area nor on the other grid hunted with snares. There was no evidence that hunting caused weight loss in hares.

4) Using the model and parameter values proposed in Chapter 2, the harvest reported for Newfoundland was not sufficient to cause the extended low believed to occur there from 1980 to the 1995.

5) The model predicted that a heavy harvest could increase the period of the hare cycle and that period was related to the intensity of harvesting at the cyclic low.

6) Pellet counts may be a useful, inexpensive way to track hare populations in Newfoundland if precautions to completely search under moss ground cover.

This is the first study to directly examine the impact of harvesting on snowshoe hare populations. I predicted there would be both long-term and immediate impacts of harvesting on snowshoe hare abundance.

I expected long-term effects on the snowshoe hare populations from harvesting to have the greatest impact during a cyclic low. Overharvesting of snowshoe hares was suggested by hunters as the reason for the observed extended low in Newfoundland snowshoe hare populations from 1979 to 1995 (Figure 1.3). My model (Chapter 2) predicted that intensive harvesting could lengthen the period of the cycle by slowing the growth of the population particular during the cyclic low. I was able to extend the low from 3 years without hunting to 5 years with 100% removal of the vulnerable prey component during the cyclic low. This is far from the 16-year low that occurred in Newfoundland. There are several possible reasons for this, one relates to the model. First, through the vulnerable and invulnerable prey components the model could have
protected too many hares. As seen in Figure 2.1, the mechanism for increasing the portion of hares vulnerable to harvesting (and natural mortality) was denoted as $vI$, however the model was insensitive to large increases in $vI$. Increasing $vI$ 100-fold only lengthened the low by 2 years. Therefore, it is likely that the complex equation for vulnerable prey needs to be revamped. Second reason for the model failing to duplicate the extended low relates to the population dynamics of snowshoe hare in Newfoundland. It is possible that hare populations did increase somewhat during the late 1980s with the decline being captured during the pellet counts of Thompson and Curran (1993). This was also supported by the small increase in the lynx harvest in 1990 and 1991. However, it would have been a damped peak because snowshoe hares were not commonly seen (K. Hodges pers. comm. 1999). If this is the case, I am still left with a 10-year low from 1979 to 1989, unless the same thing occurred in the early 1980s and was not observed. The model predicted harvesting levels that were consistent with Pepin (1987) and Allen (1938), but within my model these levels were high for a short period of time. Neither Pepin (1987) nor Allen (1938) mention the time period for which the populations were able to withstand the high harvest but indicated it was a regular occurrence.

I found evidence for immediate effects of harvesting through live-trapping. A comparison of hunted and non-hunted areas showed that, in Newfoundland, harvesting did reduce local snowshoe hare populations during a hunting season (Chapter 3). As hunting occurred during the non-breeding season, new animals were not introduced to the system. Immigration did not compensate for the reduction in hares by hunters, likely due to the large areas hunted. Although not tested in this study, natural mortality may have been lower on the heavily hunted grids, as was observed by Pielowski (cited in Pepin
During the hunting season, the hunted populations experienced greater decreases in abundance than the non-hunted areas indicating that any such compensation was not complete. However, the recovery of the hunted populations by the following fall that cannot be explained by new hares on the trapping grids provides evidence that natural mortality was reduced. In addition, the September recovery of the fall populations indicated that, at least at the cyclic peak, the decease in snowshoe hare abundance during hunting season did not negatively affect the breeding population in the following spring and summer (Figure 3.2). The ability of populations to recover from heavy harvesting during a cyclic low can only be determined by continued monitoring through the decline and low phase.

As snowshoe hares are the keystone species of the boreal forest, I expected that harvesting of hares would have long-term impacts on other species. In their exploration of the boreal forest vertebrate community, Choquenot et. al. (2001) surmised that the coexistence of several predators, namely the lynx, coyote and great horned owl, is possible despite the 25-fold changes in snowshoe hare numbers, due to the regularity of the hare cycle. From this, they suggest that lengthening the low phase of the cycle may intensify competition between predators and jeopardize their coexistence. It would follow that the insertion of an additional predator (the human hunter), particularly one that is not faced with starvation or reduced reproduction with declining hare numbers, could interfere with the natural dynamics of the predator-prey system. Based on the lynx harvest data for Newfoundland (Figure 1.2) the low hares populations had an impact on the lynx. However, lynx populations rebounded quickly following an increase in hare numbers in 1996, despite the possible extended low, the presence of great horned owls
and the intrusion of the coyote in 1985. The resilience of the lynx to depleted food supplies over a relatively long period may provide insight into how the species survived in Newfoundland prior to the introduction of the snowshoe hare.

**Future of snowshoe hare harvesting in Newfoundland**

If harvesting of snowshoe hares in Newfoundland contributed significantly to the low in hare populations from 1979 to 1995, it is unlikely we shall ever see this again. The increase in snowshoe hare populations of Newfoundland starting in 1996 coincides with the collapse of the cod fishery in 1995 and the great exodus of Newfoundlanders to mainland Canada to look for work. In 1994, prior to the fishery crisis, there were approximately 574,000 people in Newfoundland. By 2000, the population had dropped by 35,000 people to 539,000 (Newfoundland Statistics Agency 2001). The majority of the people leaving are from rural Newfoundland, where the fishery or spin-off industries were the main employers. In addition, financial assistance to relocate to Newfoundland's urban areas has been offered to some communities hardest hit by the closure of the fishery. Rural Newfoundlanders were the main harvesters of snowshoe hares, and therefore the release of the snowshoe hare by the reduction in this major predator may, at least in part, account for the recent increase in hare populations.

**Management Recommendations and Conclusions**

Although the snowshoe hare is an introduced species for Newfoundland, it has significantly influenced the shape of the forest ecosystem over the past 137 years. As the keystone species, it is a fundamental component of the present-day forest community. Management of the snowshoe hare must include a long-term population monitoring
program. Mark-recapture through live-trapping provides the best estimate of population size however the cost can be prohibitive. Material for each grid with 50 traps costs about CAN $5000. The traps were the biggest expense. It is likely that at peak populations in areas of excellent hare habitat, trap saturation will occur and additional traps will be needed to estimate the population. In addition, there was a regular requirement to replace traps due to traps being stolen or damaged. Further to this, there are labor costs to setup the grids (2-5 days work) and to trap and handle the hares.

Monitoring of hare populations using fecal pellet counts is a cheaper alternative to live-trapping but must be done in conjunction with live-trapping, until a conversion factor for the Newfoundland forest can be established (Krebs et al 2001a). I found that in areas with moss, individual hare pellets quickly disappeared within the moss. Thus, it would be necessary to thoroughly search the ground, including carefully lifting the moss to reduce damage to the site. More work should be done on pellet degradation to determine the correct interval for sampling. Pellets found in ground cover where the microclimate is moist and dark would be aged younger than those exposed to drying by the wind and sun. I suspect pellet counts would have to be done at least once per year. The length and the number of the transects needed would also have to be explored.

Krebs et al (2001b) considered that the boreal forest community in the Yukon operates predominantly as a top-down system, with predators exhibiting significant influence over hare and grouse populations but not on populations of squirrels, mice or voles. Regular monitoring of the forest predators, such as lynx or coyotes by winter track counts or great horned owls using call counts, would also provide insight into the dynamics of the forest community. The impacts of hares on vegetation in Newfoundland
have also not been examined. Comparisons between vegetation inside and outside
snowshoe hare exclosures in the Yukon indicated that hares did not have significant
impacts on the plant community within the 10 years of the Kluane study, and suggest that
it may take up to 50 years before the effects on tree species are seen.

Snowshoe hares will remain important to Newfoundlanders. Despite the recent
emigration of many rural Newfoundlanders, the ‘rabbit’ is still entrenched within our
lifestyle and harvesting will continue. Therefore, monitoring the snowshoe hare harvest
should become a priority. In conclusion, management of snowshoe hares should include
a regular monitoring program. At times of lows in the snowshoe hare cycle there should
be reductions in harvesting, possibly by shortening the season, as this is much easier to
enforce than the setting of bag or possession limits.
Literature cited


Appendix I. Sensitivity analysis for each parameter of the predator-prey model. The bold line indicates the value used in the model. I tested changes to rate of increase, predator search efficiency, predator conversion efficiency, predator death, prey carrying capacity, and predator handling time and recorded the response of peak prey and predator abundances and cycle period.

<table>
<thead>
<tr>
<th>Rate of increase (rr)</th>
<th>Peak prey abundance</th>
<th>Peak predator abundance</th>
<th>Cycle period</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.95</td>
<td>0.065</td>
<td>15</td>
</tr>
<tr>
<td>1.5</td>
<td>1.88</td>
<td>0.08</td>
<td>11.5</td>
</tr>
<tr>
<td><strong>1.89</strong></td>
<td><strong>1.85</strong></td>
<td><strong>0.093</strong></td>
<td><strong>10</strong></td>
</tr>
<tr>
<td>2</td>
<td>1.84</td>
<td>0.096</td>
<td>9.5</td>
</tr>
<tr>
<td>2.5</td>
<td>1.79</td>
<td>0.11</td>
<td>8.5</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Predator search efficiency (ap)</th>
<th>Peak prey abundance</th>
<th>Peak predator abundance</th>
<th>Cycle period</th>
</tr>
</thead>
<tbody>
<tr>
<td>65</td>
<td>1.04</td>
<td>0.071</td>
<td>None</td>
</tr>
<tr>
<td>100</td>
<td>1.35</td>
<td>0.084</td>
<td>9</td>
</tr>
<tr>
<td><strong>133</strong></td>
<td><strong>1.85</strong></td>
<td><strong>0.093</strong></td>
<td><strong>10</strong></td>
</tr>
<tr>
<td>150</td>
<td>1.98</td>
<td>0.095</td>
<td>11</td>
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<tr>
<td>200</td>
<td>2.17</td>
<td>0.099</td>
<td>12.5</td>
</tr>
</tbody>
</table>
Appendix I (con’d). Sensitivity analysis for each parameter of the predator-prey model

The bold line indicates the value used in the model. I tested changes to rate of increase, predator search efficiency, predator conversion efficiency, predator death, prey carrying capacity, and predator handling time and recorded the response of peak prey and predator abundances and cycle period.

<table>
<thead>
<tr>
<th>Predator conversion efficiency (et)</th>
<th>Peak prey abundance</th>
<th>Peak predator abundance</th>
<th>Cycle period</th>
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<tbody>
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<tr>
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<td>1.44</td>
<td>0.066</td>
<td>10.5</td>
</tr>
<tr>
<td><strong>0.05</strong></td>
<td><strong>1.85</strong></td>
<td><strong>0.093</strong></td>
<td><strong>10</strong></td>
</tr>
<tr>
<td>0.06</td>
<td>1.8</td>
<td>0.116</td>
<td>10</td>
</tr>
<tr>
<td>0.08</td>
<td>1.75</td>
<td>0.158</td>
<td>9.8</td>
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<table>
<thead>
<tr>
<th>Predator death (dp)</th>
<th>Peak prey abundance</th>
<th>Peak predator abundance</th>
<th>Cycle period</th>
</tr>
</thead>
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<tr>
<td>0.2</td>
<td>1.92</td>
<td>0.16</td>
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<tr>
<td>0.4</td>
<td>1.92</td>
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<td>15</td>
</tr>
<tr>
<td>0.6</td>
<td>1.92</td>
<td>0.12</td>
<td>11.5</td>
</tr>
<tr>
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<td><strong>1.85</strong></td>
<td><strong>0.093</strong></td>
<td><strong>10</strong></td>
</tr>
<tr>
<td>1</td>
<td>1.44</td>
<td>0.68</td>
<td>9.5</td>
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</table>
Appendix I (con’d). Sensitivity analysis for each parameter of the predator-prey model

The bold line indicates the value used in the model. I tested changes to rate of increase, predator search efficiency, predator conversion efficiency, predator death, prey carrying capacity, and predator handling time and recorded the response of peak prey and predator abundances and cycle period.

<table>
<thead>
<tr>
<th>Prey carrying capacity (K)</th>
<th>Peak prey abundance</th>
<th>Peak predator abundance</th>
<th>Cycle period</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.501</td>
<td>0.031</td>
<td>None</td>
</tr>
<tr>
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<td>0.65</td>
<td>0.048</td>
<td>None</td>
</tr>
<tr>
<td>2</td>
<td>1.31</td>
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<td>9.8</td>
</tr>
<tr>
<td><strong>2.4</strong></td>
<td><strong>1.85</strong></td>
<td><strong>0.093</strong></td>
<td><strong>10</strong></td>
</tr>
<tr>
<td>2.8</td>
<td>2.34</td>
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<td>10.5</td>
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<tr>
<td>3.4</td>
<td>3.03</td>
<td>0.14</td>
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<td>4.55</td>
<td>0.205</td>
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<table>
<thead>
<tr>
<th>Predator handling time (h)</th>
<th>Peak prey abundance</th>
<th>Peak predator abundance</th>
<th>Cycle period</th>
</tr>
</thead>
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<td>0.54</td>
<td>0.055</td>
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<td><strong>0.093</strong></td>
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<td>0.072</td>
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</table>
Appendix II. The frequency of the number of pellets per plot for sampling inside and outside the boundary to Butter Pot Park. Pellets were counted in 10x150 cm (1500 cm²) plots.

<table>
<thead>
<tr>
<th>Number of Pellets per plot</th>
<th>Inside park boundary</th>
<th>Outside park boundary</th>
<th>Total</th>
</tr>
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</tr>
<tr>
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<td>0</td>
<td>1</td>
</tr>
<tr>
<td>11</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
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<td><strong>300</strong></td>
<td><strong>600</strong></td>
</tr>
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</table>