LANDSCAPE ANALYSIS OF DISTRIBUTION AND DEMOGRAPHIC CONSEQUENCES IN A BROOD PARASITE-HOST SYSTEM

by

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ABSTRACT

Source-sink dynamics may occur where variation in predation or parasitism is sufficient to cause spatial variation in population performance. Brood parasitic brown-headed cowbirds *Molothrus ater* locally reduce host reproductive success, but little is known about their regional effects on demography. I aimed to predict, using detailed empirical data, the effect of cowbirds on the spatial dynamics of a preferred host, the song sparrow *Melospiza melodia*. My objectives were to: (1) predict the distributions of parasite and host based on landscape features; (2) predict parasitism rates from cowbird occurrence and relate this to sparrow fecundity; and (3) map expected population growth rates \( \lambda \) for song sparrows given parasitism, testing if spatial refuges from parasitism exist.

I used logistic regression to predict cowbird occurrence by analyzing >500 avian point counts in the Southern Gulf Islands (SGI), BC. I also evaluated alternate hypotheses for landscape features thought to influence cowbird distribution elsewhere. Cowbird occurrence in the SGI was best predicted by proximity to potential feeding areas and landcover. The best logistic model included landcover, cattle, and distance to urban and agriculture. Autologistic regression improved model performance, and models using widely available data performed only slightly worse than those including all data. All models of cowbird occurrence compared favorably with parasitism rates observed in 12 populations studied from 1-8 years.

To estimate the regional effect of cowbirds, I employed data from 10 islands studied from 2-8 years to estimate \( \lambda \) in song sparrow populations subject to parasitism. Predicted growth rates were strongly influenced by cowbird distribution and land use, and
were consistent with independent estimates of local population trend and findings relating parasitism rates to landscape features elsewhere in their range.

My results suggest that the ratio of source to sink populations within a study region will depend on land use patterns, their effect on cowbird distribution, and the influence of parasitism on host reproduction. I use my results to suggest improvements for future habitat modelling studies, management to limit cowbird distribution and identify host refuges, and an approach to estimate the regional effect of enemies on the spatial population demography of species of conservation concern.
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Chapter 3 is being prepared for submission to a scholarly journal, under the same title. The co-author of this chapter is Dr. Peter Arcese. K. J. Jewell performed all analyses and wrote the manuscript. The co-author performed preliminary data analysis and gave statistical advice and editorial assistance.
CHAPTER 1:  
INTRODUCTION

Spatial structure of populations in ecology and conservation

Understanding the habitat associations of species has become a goal in ecology and conservation management because landscape context and local habitat attributes influence the abundance of species and persistence of populations (Gilpin & Hanski 1991). In this thesis, I examined the spatial distributions of a parasite and a preferred host via habitat models and test for spatial variation in population performance of the host due to the impact of parasitism.

Constraints on sampling large areas often cause ecologists to rely on statistical models to predict species distributions based on local or landscape habitat attributes (e.g., species distribution models, habitat selection models, or resource selection functions), assisted by Geographic Information Systems (GIS) and spatial and remotely sensed data. Conservation planners used GIS-based habitat models to identify secure populations of threatened species such as the Mt. Graham red squirrel Tamiasciurus hudsonicus grahamensis (Pereira & Itami 1991), great bustard Otis tarda (Osborne et al. 2001), and northern pygmy owl Glaucidium californicum (Priorecky & Prescott 2006), to identify potential habitat for exotic invaders such as the monk parakeet Myiopsitta monachus (Munoz & Real 2006) and aoudad Ammotragus lervia (Cassinello et al. 2006) in Spain, and to predict the re-colonization of wolves Canis lupus in North America (Mladenoff et al. 1995; Carroll et al. 2006). However, the wide array of modelling approaches now available also makes the process of selecting and implementing the best statistical approach difficult because opinions differ on how to account for autocorrelated data and identify habitat features influential of local demography (i.e. Fielding & Bell 1997;

Spatial structure also influences population dynamics, as habitat-specific demographic rates, such as survival and fecundity, result in some populations not producing enough recruits to sustain themselves (sinks), which then have to rely on immigrants from more productive populations (sources; Pulliam 1988). Accordingly, recent critiques urge ecologists to integrate simple habitat models with more dynamic processes such as population dynamics, species interactions, and longer-term forecasts under uncertainty (i.e. climate change; Guisan & Thuiller 2005). The need to understand the effects of landscapes on population demography becomes more pertinent in light of increasing human modification and fragmentation of these landscapes, causing more species to exist as small populations linked by dispersal and subject to source-sink dynamics (Pulliam 1988; Hanski & Gilpin 1997). To predict the consequences of variation in spatial structure on the regional dynamics of natural populations, we must first understand the spatial variation in local population performance (Pulliam & Danielson 1991; Donovan et al. 1995b).

Ecological theory suggests that the spatial structure, dynamics and coexistence of populations will be influenced by the distribution of enemy competitors, predators, or parasites (i.e. see Tilman & Kareiva 1997). For example, Namba et al. (1999) evaluated the persistence of populations with predators and competitors under different configurations of and connectivity between sources and sinks. Barabás et al. (2004) developed a source-sink model to demonstrate potential stabilization of a parasite-host relationship using the specialist brood parasite the common cuckoo *Cuculus canorus*. 
Other studies have examined the population performance of forest-dwelling birds, using habitat (degree of fragmentation) as a surrogate for rates of parasitism and predation (Temple & Cary 1988; Donovan et al. 1995a; Lloyd et al. 2005). However, I am aware of no studies synthesizing these approaches or using empirical data to examine the spatial demography of a species as a function of the distribution of their enemies.

Effects of cowbird parasitism on hosts

I studied the demographic effect of parasitism by brown-headed cowbirds *Molothrus ater* on a preferred host species in a naturally fragmented landscape, the Southern Gulf Islands, British Columbia, Canada (SGI). This system is ideal for my purposes because: (1) brown-headed cowbirds have a clear spatial distribution that should make spatial patterns of parasitism predictable; and (2) there is evidence that the host species, the song sparrow *Melospiza melodia*, persists with source-sink dynamics in the study area.

Brown-headed cowbirds are brood parasites that have been implicated in the decline of numerous songbird populations (Mayfield 1977) and reduce reproductive rates in many host species (i.e. Robinson et al. 1995; Kus & Whitfield 2005). Cowbirds have invaded much of their current range in the last century (Rothstein 1994), reaching coastal British Columbia in the 1950s (Peterjohn et al. 2000). Thus, cowbirds may pose a relatively new threat to potential hosts in these regions.

As generalists, cowbirds have been documented to parasitize over 200 different host species (Lowther 1993). Cowbirds reduce the reproductive output of hosts by removing host eggs (Sealy 1992), inducing abandonment of parasitized nests (Ortega &
Ortega 2001), out-competing host species nestlings for parental care (Hauber 2003), and depreating unparasitized nests (Arcese et al. 1996). Due to their negative effects on hosts, cowbirds can influence decisions about land use and conservation policy. However, the effect of cowbirds on host population dynamics and persistence is not well understood.

Because cowbirds are brood parasites and do not spend time tending to a nest, breeding and feeding activities can be separated spatially and temporally. Radio-tracking studies have illuminated the typical daily behavior of cowbirds: in the morning they search for potential hosts in the nest-building or laying stage; then, in the afternoon, they fly to feed in short grass habitats, which include grazed fields, lawns, and other openings, or at bird feeders; and in the evening, they roost communally, resulting in large overall home ranges (Rothstein et al. 1984; Thompson 1994; Goguen & Mathews 2001).

Cowbird distribution and abundance has been linked to the amount and spatial configuration of these feeding and breeding habitats (Tewksbury et al. 1998; Chace et al. 2005). It is clear that cowbird abundance declines when the commuting distance to feeding habitat exceeds 3 km, and approaches zero more than 7 km to feeding areas (Rothstein et al. 1984; Thompson 1994; Gates & Evans 1998; Curson et al. 2000; Goguen & Mathews 2001). Land conversion by humans can facilitate cowbirds by creating habitat features that bring them into proximity with vulnerable hosts (Coker & Capen 1995; Chace et al. 2003), suggesting that they are human commensals. Both the abundance of cowbirds and the parasitism rates of their hosts appear to be influenced by landscape-level factors, but it is not yet known how landcover and the configuration of
these different habitats affect the spatial dynamics of cowbird parasitism in complex
natural and human-modified landscapes (Gustafson et al. 2002).

I chose the song sparrow because it is a preferred host (Lowther 1993; Scott &
Lemon 1996), and a ubiquitous open cup nester similar to many other host species
(Arcese et al. 2002). The song sparrow was the subject of one of the earliest and most
thorough avian behavioral studies (Nice 1937), and since then has built a reputation as a
model species furthering the study of various biological disciplines (Arcese et al. 2002;
Smith et al. 2006). For nearly 40 years, song sparrows have been studied on six-hectare
Mandarte Island, BC, Canada, generating an understanding of the driving factors in the
system that is almost unrivaled (Smith et al. 2006). Findings from this model system are
widely cited in Ecology textbooks and have been applied by conservation biologists to
manage threatened and endangered species in small and isolated populations.

One key factor affecting song sparrow population dynamics is the brown-headed
cowbird, which limits sparrow populations via a combination of parasitism and predation
(Arcese et al. 1996; Arcese & Smith 1999). High parasitism rates (~60-80%) in the
Fraser River Delta, BC, created population sinks ($\lambda < 1$) (Smith et al. 1996; Rogers et al.
1997). Population growth rates in these areas only became self-sustaining ($\lambda > 1$) when
cowbirds were experimentally removed (Smith et al. 2002). There is also much evidence
that spatial variation in the intensity and frequency of parasitism exists among
populations of song sparrows (Smith & Myers-Smith 1998; Wilson & Arcese 2006).
Study objectives

My overall objectives in this thesis were to: (1) identify the potential distributions of both cowbirds and song sparrows; (2) predict potential parasitism rates based on landscape features influencing cowbird distribution; (3) relate song sparrow reproductive output to cowbird parasitism rates; and (4) predict and map potential population growth rates for song sparrows considering the impact of parasitism (Figure 1.1).

In Chapter 2, I concentrate on habitat modelling for brown-headed cowbirds, with two principle goals. First, I test which landscape features predict cowbird occurrence, and use this to create a predictive distribution map. Second, I use this as a case study to evaluate a suite of techniques comprising a robust approach to species habitat models. I correct for spatial autocorrelation, validate models, and evaluate models created from datasets varying in cost and availability. Cowbirds make a relevant case study because their distribution seems to be strongly affected by landscape features and their potential effects on host species makes them of interest to managers.

In Chapter 3, I aim to determine whether there are spatial refuges where hosts may be free from parasitism pressure. I use avian surveys, GIS, an extensive empirical dataset, and habitat and population modelling to predict the demographic effect of cowbird parasitism on a preferred host species. The final product is a map predicting population growth rates of song sparrows within the 1,500 km² study area in the Southern Gulf Islands. In Chapter 4, I summarize my results, suggest future research directions, and discuss the implications of this research for conservation.
Figure 1.1: Flow chart of the thesis. The key endpoint is a map of the expected population growth rate of song sparrows considering the impact of parasitism. Chapter 2 develops the habitat modelling techniques leading up to the cowbird map, while Chapter 3 combines the predictive maps with empirical population data to examine the effect of cowbirds on song sparrows.
References


CHAPTER 2: 
ROBUST SPECIES HABITAT MODELS FOR PREDICTING THE DISTRIBUTION OF BROOD PARASITES

Introduction

Predicting the distribution of species is a goal in ecology and, increasingly, a requirement for effective conservation and management. However, habitat selection models frequently violate the assumption of independent observations because survey points are spatially autocorrelated. Spatial autocorrelation is a property in which a pair of sites a given distance apart are either more or less similar (positive or negative autocorrelation, respectively) than expected given a random pair of observations (Legendre & Legendre 1998). Both environmental and species data are often autocorrelated due to geographical gradients, ecological processes (e.g., spacing and dispersal patterns), and the scale of analyses, and all of these conditions can be expected to influence analyses based on these data (Legendre 1993). For example, habitat models based on autocorrelated data will generally overestimate the importance of environmental variables in predicting species occurrence (Cliff & Ord 1981; Legendre 1993). The autologistic model, which explicitly models autocorrelation by including an autocorrelated error term in the regression model (Augustin et al. 1996), corrects for these biases and is increasingly implemented in ecological studies. Further, these studies have shown that autologistic habitat models have more predictive power than do standard logistic models (Osborne et al. 2001; Klute et al. 2002; Lichstein et al. 2002; Betts et al. 2006).

1 A version of this chapter will be submitted for publication. Jewell, K.J., Arcese, P., and Gergel, S.E. Robust species habitat models for predicting the distribution of brood parasites.
Developing predictive distributions is particularly important in the case of invading species, which can cause severe ecological and economic damage to ecosystems (i.e. Pimental et al. 2000). Brown-headed cowbirds *Molothrus ater* are obligate brood parasites that invaded much of their current range in the last century, reaching the Georgia basin of British Columbia around 1955 (Rothstein 1994; Campbell et al. 2001). Because cowbirds are implicated in the decline of numerous songbird populations (Mayfield 1977) and reduce reproductive rates in many host species (i.e. Robinson et al. 1995a; Smith et al. 2002; Kus & Whitfield 2005), their invasion has the potential to reduce populations of susceptible hosts and to influence decisions about land use and conservation policy.

In this paper, we used cowbirds as a case study to evaluate a suite of techniques comprising a robust approach to species habitat models, including correcting for spatial autocorrelation. Cowbirds make a relevant case study because their distribution and abundance and the parasitism rates of their hosts seem to be strongly affected by landscape features and their effects on host species make them of interest to managers. Land conversion by humans can facilitate cowbirds by creating habitat features that bring them into proximity with vulnerable hosts (Coker & Capen 1995; Chace et al. 2003). In particular, cowbird distribution and abundance has been linked to the amount and spatial configuration of feeding and breeding habitats (Tewksbury et al. 1998; Chace et al. 2005). Because cowbirds are parasitic and thus do not spend time tending to a nest, breeding and feeding activities can be separated spatially and temporally. Typically, cowbirds search for potential hosts in the morning, then fly to feed in short grass habitats, which include grazed fields, lawns, and other openings, or at bird feeders, resulting in
large overall home ranges (Rothstein et al. 1984; Thompson 1994; Goguen & Mathews 2001). It is clear that cowbird abundance declines when the commuting distance to feeding habitat exceeds 3 km, and approaches zero over 7 km from feeding areas (Rothstein et al. 1984; Thompson 1994; Gates & Evans 1998; Curson et al. 2000; Goguen & Mathews 2001), but it is not yet known how landcover and the configuration of feeding and breeding habitats affect the spatial dynamics of cowbird parasitism in complex natural and human-modified landscapes (Gustafson et al. 2002).

We set out to predict cowbird distribution across a 1,500 km\(^2\) landscape in southwestern British Columbia (BC), Canada, extending previous work in specific habitats (Coker & Capen 1995; Gustafson et al. 2002). We tested if landcover and habitat configuration influenced cowbird distribution, and tried to identify landscape features that might facilitate land management decisions to reduce parasitism. Using habitat modelling within a Geographic Information System (GIS) framework, we corrected for spatial autocorrelation and applied robust evaluation and validation methods to address recent critiques of habitat models (Fielding & Bell 1997; Guisan & Zimmermann 2000; Rushton et al. 2004; Gottschalk et al. 2005; Guisan & Thuiller 2005; Araujo & Guisan 2006; Betts et al. 2006). Our goals in this paper were two-fold: to examine the spatial distribution of cowbirds in our study landscape and to use this system as a model to evaluate a suite of newer approaches in habitat modelling.

We first asked how well local and landscape features predicted brown-headed cowbird occurrence by comparing sets of variables representing landscape configuration, landcover, and local factors. To do so, we used cowbird presence in point count surveys and univariate relationships to examine the effect of individual landscape features as well
as measures of host community composition, which may also affect spatial decisions by cowbirds (i.e. Young & Hutto 1999). We also compare a set of models, outlined in Table 2.1, that differ in their assumptions about how cowbird distribution is linked to spatial variation in the abundance and configuration of feeding and breeding habitats in the landscape. Potential cowbird feeding grounds in our study area included agricultural land, farms with cattle, and suburban areas. We also considered the distance to the nearest urban area, the town of Sidney on the Saanich Peninsula of VI (population 11,000), which has been considered a likely source of cowbirds regionally and successfully related to variation in cowbird parasitism rates in the region (Smith & Myers-Smith 1998; Wilson & Arcese 2006).

Second, we asked if it is possible to accurately predict and map the presence of cowbirds using landscape variables. We used landscape variables and logistic regression to identify a “best” habitat selection model based on its fit to empirical data. To account for spatial autocorrelation, we used the state-of-the-art technique of the autologistic model (Augustin et al. 1996). We compared the predictive power among a suite of models that do or do not correct for spatial autocorrelation, as well as models based on widely available datasets. Many studies have compared the utility of local-scale intensive ground surveys to landscape-scale GIS data (e.g. Saveraid et al. 2001; Seoane et al. 2004; Betts et al. 2006). However, even within landscape-scale data, there are differences in cost and availability. Thus we compared the power of our best models, which contain data from costly field and proprietary sources, to simpler models based on datasets easily accessible to managers and available across broad geographic regions. Such information is of particular use to practitioners looking to extrapolate the results of habitat distribution
studies. Finally, we assessed our models using an independent dataset of parasitism rates of a preferred host species in a novel and comprehensive validation.

Materials and Methods

Study Area

We studied patterns of cowbird distribution in the Southern Gulf Islands (SGI), located in the Strait of Georgia to the southeast of Vancouver Island (VI), Canada. The area has a mild Mediterranean climate, and vegetation falls predominately into the Coastal Douglas Fir *Psuedotsuga menziesii* biogeoclimatic zone. Many smaller islands are vegetated by sea island scrub. The study area is about 70% forested, 13% rural, 6% agriculture, 2% suburban/urban, and 9% other (Islands Trust Ecosystem Mapping Project). Our study area was the southern portion of the SGI, measuring approximately 27 x 57 km (123°00' W, 48°32' N; Fig. 2.1). The study area includes over 100 islands, ranging in size from tiny islets to 186 km²; in total they comprise roughly 380 km².

Bird Surveys

We conducted avian point counts throughout the SGI between 6 May and 10 July 2005. Cowbirds tend to arrive in the region in late April, and their breeding season ends in mid-July (Smith et al. 2006b); thus, the dates of our study are well within the breeding season of local cowbirds. Counts were ten minutes in duration, and took place between 0600 and 1100 hrs, when cowbirds frequent breeding sites (Smith & Arcese 1994). Point counts were conducted by 1-2 trained observers. We recorded weather variables for each count and excluded outliers due to more extreme events.
We used all cowbirds detected within 100 m and during both the standard 10-min count plus the subsequent period while we used playbacks for a common host as part of a concurrent study (an additional 3-min). We found no difference from models using more selective counts of cowbirds (10-min count and 50 m radius), thus proceeded to use all cowbirds detected in order to increase our power to detect differences in occupied and unoccupied sites. We did not include playbacks for cowbirds as Miles and Buehler (2000) showed that playbacks did not improve detection success.

We stratified the location of counts in order to sample cowbirds in all landcover classes available in GIS layers, with the number of counts per island roughly proportional to island size. Each point count location was visited only once; previous studies have shown single-visit surveys to adequately represent the breeding species present (Haila & Kuusela 1982). We did make repeat counts \( n \approx 8 \) on several small islands for a concurrent study; these counts were all included in our analyses, but their inclusion made little difference to model selection or parameterization.

We aimed to space all counts at least 200 m apart, but as cowbirds are highly vagile with large home ranges, we cannot confirm that counts were independent of each other. We attempted to correct for any lack of independence by explicitly measuring and incorporating spatial autocorrelation into our habitat models. Point count locations were recorded using a handheld GPS device (GPS60, Garmin Ltd, Kansas, USA), with each recorded point the result of at least 100 GPS positions to improve accuracy. Once in the GIS, the GPS locations were checked against orthorectified aerial photographs.

Total avian species richness and suitable host richness were estimated from the point counts. Suitable hosts were defined as open-cup nesters known to accept cowbird
eggs and feed mainly arthropods to their young (De Groot & Smith 2001). We also used
song sparrow *Melospiza melodia* abundance as potential predictor variable since they
were the most prevalent host in the area.

**LANDSCAPE VARIABLES**

Candidate predictor variables were chosen based on their importance to brown-
headed cowbirds, subject to availability, and were derived from point counts, available
GIS coverages, and a Landsat image (Table 2.2). Two spatial datasets represented
vegetation for the study area. First, the Islands Trust Ecosystem Mapping project
interpreted digital orthophotos of the islands from 2000 and 2002 (accurate to 10 m;
Islands Trust, Victoria, BC), classifying them into 13 classes, which we collapsed into
seven (Table 2.2). Second, we had a Landsat-7 Enhanced Thematic Mapper image with a
25m resolution that used 23 classes, and which we collapsed into eight basic landcover
types (EOSD/Canadian Forest Service, 2000; Table 2.2). We also collapsed the Landsat
image into a binary classification of forest/nonforest, as well as an ordinal variable
representing four levels of crown closure. This coarse-level canopy closure variable
(CCS) was contrasted with a finer one (CCL) created based on a 0.5 m black and white
digital orthophotos (Integrated Mapping Technologies, Vancouver, BC, 2002) used to
classify canopy cover into 10% increments from 5% to 95% closure within a 100 m
radius of each point count location.

Landscape variables were created using ArcGIS 9.1 and its Spatial Analyst
extension (ESRI Inc., Redlands, CA, 2005) by calculating the proportion of each feature
within a 2.5 km radius as well as nearest distance to that feature (context and distance
variables, respectively; Table 2.2). We chose a 2.5 km distance for the context variables
as an average commuting distance (after Gustafson et al. 2002). An additional set of variables describing the distribution of agriculture was created using data from the Agricultural Land Reserve (ALR; Provincial Agricultural Land Reserve, Burnaby, BC). Because cowbirds are often associated with cattle, but the locations of livestock were not available as a spatial layer, we consulted local veterinarians to map the locations of cattle, corroborated these locations by site visits and digitized them as polygons to create data layers of distance to and proportion of cattle as described above. Cowbirds also associate with horses in California and the SGI (Rothstein et al. 1984; our obs.) but were too ubiquitous to map reliably.

We also included available landscape information within about 10 km of the study area to minimize the influence of edge effects on our model predictions at study area boundaries. We added information for cattle on the Saanich Peninsula of VI by recording their locations during thorough searches by car. We added information for VI suburban areas and agriculture by digitizing polygons in a manner consistent with the Ecosystem Mapping project, using 0.5m color digital orthophotos.

STATISTICAL ANALYSES

Because few variables were normally distributed we used a combination of nonparametric tests and variable transformations for statistical analysis. To test for relationships between cowbird presence and independent variables representing local and landscape features, we compared count locations with and without cowbirds detected using Mann-Whitney U-tests and corrected for multiple comparisons using Bonferroni's correction (Legendre & Legendre 1998). Because not all landscape variables were available for Vancouver Island, these counts were excluded from analyses.
We used logistic regression to evaluate our competing hypotheses about the landscape factors that control cowbirds (Table 2.1) after converting count data to presence/absence and transforming variables to approximate normality. Distance variables were loge or square root transformed while proportion variables were arcsine-square-root transformed. Logistic regression models the logit of probability of occurrence of cowbirds (p,) as a linear function of the independent variables. Candidate models were evaluated using an information theoretic approach and Akaike’s Information Criterion (AIC; Burnham & Anderson 2002).

To determine how well we could predict and map cowbird distribution, we created a ‘best logistic’ model using only candidate variables with continuous GIS coverage. We used an interactive forward stepwise procedure entering variables with the lowest significance values for their score statistics to a P = 0.10 cutoff (SYSTAT 11.0, SYSTAT Software Inc, San Jose, CA). To avoid collinearity, candidate variables correlated (r ≥ 0.60) with variables already entered were not allowed in the model. To evaluate the use of only widely available datasets, we used the same stepwise procedure to create a ‘best simple’ model using only Landsat and Agricultural Land Reserve data.

To correct for spatial autocorrelation, we followed Augustin et al. (1996) by using an autologistic model and modified Gibbs sampler. Starting with our best logistic model, we added an additional term, the autocovariate, to account for spatial dependencies in the data, calculated as:

$$\text{autocov}_i = \frac{\sum_{j=1}^{k_i} w_{ij} \hat{p}_j}{\sum_{j=1}^{k_i} w_{ij}}$$

Eqn. 2.1
where $w_{ij}$ represents the inverse Euclidean distance between points $i$ and $j$, and $p_j$ is the predicted probability of occurrence at point $j$ (Augustin et al. 1996). The autocovariate represents the weighted average of the predicted probability of occurrence for a given set of $k_i$ neighbors, and corrects predicted values accordingly.

To determine the best neighborhood size, we compared models with a range of neighborhood sizes. We defined the first order neighborhood as all neighbors within a 200 m distance of point $i$, and additional neighborhoods were created by adding neighbors at successive 200 m intervals to 1600 m, using Spatial Analyst in ArcGIS. Because we only sampled a small part of the available landscape, the modified Gibbs sampler generated species' response in unsurveyed cells (Augustin et al. 1996).

We tested for spatial autocorrelation in the independent variables and raw occurrence data using Moran's $I$ correlograms. We used a total of 20 lags separated by 300 m (from 0-300 m to 5700-6000 m); each lag interval had a sufficient number (>1000 pairs) of points to provide enough power to detect spatial pattern. Moran’s $I$ typically falls between 1 and -1, with positive and negative values indicating positive and negative spatial autocorrelation, respectively. An expected value at 0 indicates no autocorrelation. Statistically significant spatial autocorrelation was identified using Monte Carlo simulations with 999 permutations to estimate the probability of obtaining the observed Moran’s $I$ value at each lag, the significance of which was assessed by a progressive Bonferroni correction (Legendre & Legendre 1998; Lichstein et al. 2002). We created Moran’s $I$ correlograms to examine autocorrelation in residuals of regressions but we did not test for significance because the appropriate null model was not available (see Lichstein et al. 2002). All tests for spatial autocorrelation and of autologistic models
were done using R2.3.1 (R Development Core Team, 2006) and the ‘spdep’ (R. Bivand, 2006) and ‘Design’(F. E. Harrell Jr., 2005) packages.

There are many different ways to assess the performance of models predicting species’ occurrences; we used four main statistics to compare among models and to select the best autologistic model. We used relative AIC scores to compare among models; models with a ΔAIC <2 are considered to have good support (Burnham & Anderson 2002). Goodness of fit was assessed using Nagelkerke’s R² index, which approximates the R² of least squares regression models (Nagelkerke 1991; Hosmer & Lemeshow 2000). We used another measure, the Hosmer-Lemeshow goodness-of-fit statistic, which employs a Chi-squared type distribution to compare observed versus expected model outcomes (Hosmer & Lemeshow 2000). The null hypothesis is that the fit of the model is adequate. The models’ discrimination power was also assessed using receiver operating characteristics (ROC) plots. ROC plots are increasingly used by ecologists in recognition that model evaluation based on an arbitrary cut-off of predicted probability > 0.5 is often not ecologically suitable (e.g. Fielding & Bell 1997; Gibson et al. 2004). The area under the curve (AUC) of the ROC plot indicates overall fit of the model and varies from 0.5 (no better than chance) to 1.0 (perfect discrimination). Models are considered to have high discrimination power if AUC > 0.70 (Hosmer & Lemeshow 2000).

MAPPING AND MAP COMPARISON

Predictive distribution maps were created for the final three models by combining the input layers in a raster (grid-based) GIS with a 25m resolution, showing probability of cowbird occurrence within each pixel of the study area. To compare the spatial predictions of models, we compare maps visually and quantitatively using new
techniques for fuzzy-set map comparison. We used a method outlined by Hagen (2003) using the Map Comparison Toolkit (Research Institute for Knowledge Systems, 2004; Visser & de Nijs 2006). The advantages of using an automated method to compare maps are objectivity, evaluation, and repeatability (Hagen 2003). Fuzziness here implies a level of uncertainty, and is used both in terms of category and location.

We classified the maps of probability of cowbird occurrence into deciles, and accounted for fuzziness by location (spatial variability and noise) with an exponential decay function with a two-cell halving distance and a neighborhood with a four-cell radius (Hagen 2003). The fuzziness by category was incorporated into a category similarity matrix, with values sequentially decreasing by 0.2 by row and column. For each map comparison we reported global values for a fuzzy modification of the Kappa statistic ($K_{Fuzzy}$), the fuzzy version of fraction correct (Similarity), and the absolute value of the difference between two maps based on a cell-by-cell comparison of the continuous probability surfaces ($\text{Diff}_{abs}$).

MODEL VALIDATION

Many models lack an independent assessment of model performance, which is particularly important if predictions are to be extrapolated. We validated our models in two ways. First, we used the bootstrap method, an internal validation procedure, to evaluate our final three models. Through resampling with replacement within the dataset, the bootstrap estimates the amount of optimism in model performance statistics and adjusts these estimates accordingly. This is an effective validation method because the mean from these bootstrapped samples approximates the mean of the population (Sokal & Rohlf 1985) and it provides the most precise estimates of classification.
accuracy (Verbyla & Litvaitis 1989). We ran 1000 replications and report the bias-adjusted statistics: $R^2_{\text{corr}}$ and $AUC_{\text{corr}}$. We also report $E_{\text{max}}$, which is the maximum absolute difference in predicted and calibrated probabilities (F. E. Harrell Jr., 2005,
Design package). We chose not to partition our data to create our final models in order to not lose discrimination power (Rencher 1995).

Second, we used an independent dataset comprised of cowbird parasitism rates of song sparrows on 12 islands in the study area studied from 1 to 8 yrs from 1998-2004, following well-established methods (Wilson & Arcese 2006; Smith et al. 2006). To account statistically for variation in parasitism among years, we estimated expected mean rate of parasitism using island as a fixed effect in analysis of variance (ANOVA) on parasitism rate with year and season length as covariates. We then compared these expected mean parasitism rates to the probability of cowbird occurrence on each of these 12 islands from each of our three final predictive models using simple regression and $R^2$ as the measure of agreement between our model predictions and long-term observations of parasitism in the field.

**Results**

In the ten weeks of surveys in 2005, we conducted 531 avian point counts on 35 different islands in the SGI (Fig. 2.1). Of these, we used 477 counts for the analyses below. Cowbirds were present in 135 counts (28%). When cowbirds were present, we detected a mean of $1.59 \pm 0.08$ cowbirds per site (range 0 - 5). By including all cowbirds detected at a site, we increased the number of positive occurrences from 112 to 135 and reduced the rate of type II errors.
PREDICTORS OF COWBIRD OCCURRENCE

Sites occupied by cowbirds had higher species richness, suitable host richness, and host (song sparrow) abundance than unoccupied sites (Table 2.3), but also had higher nonhost richness (species richness - suitable host richness; \( U = 19334.5, P < 0.005 \)). Cowbirds also preferred sites with lower levels of canopy closure. The ordinal Landsat canopy closure variable (CCS) was closely related to canopy closure measured locally (CCL), and both variables showed the similar trends. Most other landscape variables also differed between occupied and unoccupied sites, but only a few comparisons retained significance after Bonferroni corrections (Table 2.3). Cowbirds were three times more likely to occur within 5 km of the nearest urban area than further away. Cowbirds were much more likely to occur closer to Vancouver Island and in areas with a lower proportion of forest. Cowbirds may also have preferred edge habitats, as they were more likely to be closer to forest and also to non-forested patches, these variables being strongly negatively related (\( r_s < -0.80 \)). More landscape context variables were significantly different between occupied and unoccupied sites than distance variables with respect to feeding areas (Table 2.3). Cowbirds preferred areas with more cattle and suburban, less agriculture, and were encountered more often further from agriculture.

To compare alternate hypotheses about which landscape features determine cowbird occurrence, we ranked a priori models by their AIC score (Table 2.4). Our best-supported model was the GLOBAL model, which contained all variables in the other models. The six other models had limited support (\( \Delta \text{AIC} > 2 \)) but AUC > 0.5, indicating that all models discriminated between occupied and unoccupied sites better than expected at random. Other models, ranked by AIC score from most to least support were:
LANDSCAPE > FEED > CONTEXT > COVER > LOCAL > BREED, the last three having little support. These a priori models explained between 2-30% of the variation in cowbird occurrence.

**EVALUATION OF HABITAT MODELS**

The best logistic model included DURB, DAG, PCAT and EM landcover and explained 24% of the variation in cowbird occurrence (Tables 2.5-2.6). The agreement between the model and occurrence data was good (AUC = 0.767), despite a poor fit to the data overall (\( \hat{C} = 12.98, P = 0.04 \)). The best simple model, using only widely available data, contained three variables: LSAT for landcover, DFOR, and DURB (Table 2.7), sharing only DURB with the best logistic model. This model performed only slightly less well than the best logistic model (Table 6), but was also of questionable fit (\( \hat{C} = 13.24, P = 0.07 \)).

All candidate autologistic models had lower AIC scores and explained a higher proportion of the variation in the occurrence data than the best logistic model, but discrimination power (AUC) of logistic and autologistic models was similar (Appendix 1). The best autologistic model had a neighborhood size of 1,200m (Appendix 1). Full iteration of the autologistic model with the modified Gibbs sampler stabilized parameter estimates, but only minimally improved model performance (Tables 2.5-2.6). Performance of the best autologistic model was slightly better than the best logistic model (Table 2.6), but the autologistic model displayed substantially improved fit (\( \hat{C} = 6.44, P = 0.49 \)). Incorporating an autocovariate term resulted in two environmental predictors having reduced statistical significance (\( P > 0.10 \); DURB and PCAT), but no change in landcover categories (Table 2.5).
MAP COMPARISON

Our logistic and autologistic models both show spatial similarities by predicting higher probabilities of cowbird occurrence in a belt from the southwest to east-central part of the study area, under the strong influence of the DURB variable (Figs 2.2-2.3). The best simple model shows more fine-scale patterning (Fig. 2.4). None of the models predict cowbirds in the northern quarter of the study area, and the models differ most in their predictions for the largest island in the SGI (Salt Spring).

As expected, maps based on the autologistic and best logistic models were most similar ($K_{\text{Fuzzy}} = 0.578$, Similarity = 89%; Logistic vs. Simple: $K_{\text{Fuzzy}} = 0.141$, Similarity = 78%; Autologistic vs. Simple: $K_{\text{Fuzzy}} = 0.066$; Similarity = 76%). The autologistic model made similar predictions to the logistic model over the northern half of the study area, but concentrated its predictions of high cowbird occurrence in the small islands around the Saanich Peninsula and at the eastern end of the study area (Samuel Island). This caused the autologistic model to under-predict slightly as compared to the logistic model ($\text{Diff}_{\text{abs}} = 5.5\%$). The best simple model differed from the autologistic and logistic models by 13% and 12%, respectively ($\text{Diff}_{\text{abs}}$), with slightly higher predictions of cowbird occurrence than these other models.

SPATIAL AUTOCORRELATION

Our raw data on cowbird occurrence and the independent variables in our best models were spatially autocorrelated (Fig. 2.5), leading to our use of autologistic regression. Moran’s $I$ correlograms for Pearson’s residuals of all three best models showed that both logistic models exhibited spatial structure, especially in the first two distance lags (to 600 m), while residuals of our autologistic model showed a 30%
reduction in Moran’s I values compared to the best logistic model at these distance lags (Fig. 2.6).

MODEL VALIDATION

Bootstrapping of the autologistic model showed that it was robust to resampling, with the maximum change in predicted probability of occurrence being less than 5%, variance explained dropping less than 2%, and the adjusted AUC still suggesting high discrimination power (Table 2.6). Although still indicating satisfactory performance, bootstrapped values of statistics for our best logistic and simple models decreased slightly more.

Our adjusted estimates of cowbird parasitism in song sparrows increased linearly with the predicted probability of cowbird occurrence of our three best models, without obvious over or under prediction (Fig. 2.7). Ordered by $R^2$ value, models from best to worst fit were the logistic ($R^2 = 0.61$), simple ($R^2 = 0.58$), and autologistic ($R^2 = 0.52$), but our autologistic model approximated the slope of the empirical relationship most closely ($b_{auto} = 83.3$ vs. $b_{log} = 65.4$ and $b_{simple} = 55.1$). All models estimated a non-zero probability of cowbird presence ($P(cowbird) \sim 0.25 - 0.52$) at one site where no parasitism was recorded from 1998 to 2005, but did occur in 2006 (our obs.).

Discussion

Our ability to understand how landscape features affect cowbird distribution and abundance is limited by the quality and concordance of results reported to date, but this uncertainty has the potential to impede the development of reliable land use policy to minimize the impact of cowbirds on host demography. Our results suggest landscape
factors influence cowbird distribution, and likely host parasitism, in island ecosystems of southwest BC. Cowbirds were best predicted by landcover, configuration, local variables and especially the proximity to urban and other feeding areas. Our habitat models demonstrated that landscape variables can be used to make reasonably accurate predictions about cowbird occurrence and were robust to internal and external validation. All predictive models showed a good fit with an independent dataset of rates of parasitism of a host species, suggesting that cowbird distribution models could be used to predict impacts on hosts. We demonstrated that autologistic models did help correct for spatial autocorrelation and improve predictive power, although all three models performed similarly overall. Models built from widely available datasets performed only slightly poorer than models from more costly and proprietary data. This simple model has the advantage that it could be applied and tested at other sites more easily, but it may be less informative for a manager interested in land use decisions.

**PREDICTING COWBIRDS WITH LANDSCAPE FEATURES**

Cowbird occurrence was best predicted by a combination of local-scale, landcover, and landscape configuration variables, although the latter seemed to have an especially large influence. The probability of detecting cowbirds increased with more cattle-grazing and suburban and less agriculture and forest. These effects were clearer with landscape context than with proximity (Table 2.3). Interestingly, tests of these hypotheses via the alternative models indicated the opposite, as the model representing proximity had more support than the model representing landscape context (Table 2.4). This result seems largely influenced by distance to urban, and, paired with the variable selection of 'best' models, also suggests that important variables in univariate analyses
are not always those leading to the highest predictive power of models. In terms of local
host community, cowbirds were more likely to be detected in areas with higher total
species, not just host, richness, and with higher abundance of a preferred host species
(Table 2.3), but the LOCAL model was not well supported (Table 2.4). These results
corroborate other studies finding that distance from feeding sites appears to have a bigger
influence on cowbird abundance at breeding sites than either landcover or host
community measures (Tewksbury et al. 1999; Young & Hutto 1999; Goguen & Mathews

The influence of distance to urban on cowbird occurrence is in line with our
predictions, but is much stronger than expected. Previous studies on song sparrow
dynamics in the study area have shown a gradient of parasitism pressure among islands,
increasing with distance to urban area (Smith & Myers-Smith 1998; Wilson & Arcese
2006). We suggest that this urban area, the town of Sidney, acts as a source for cowbirds,
providing many potential short-grass feeding areas through a wealth of lawns and
pastures as well as an airport and a horse racetrack. Distance to Vancouver Island is not
as influential, perhaps because the majority of the island’s southeast is a mixed matrix of
forest, agriculture, and rural. Strong evidence for a relationship between cowbirds and
urban (Chace et al. 2003) and suburban/rural (Tewksbury et al. 2006) areas, presumably
due to their use as foraging areas, has been established in previous studies.

Our results also suggest that cattle and suburban areas provide feeding areas for
cowbirds, but that they avoided agricultural areas as identified in both of data sources we
employed (ALR and Ecosystem Mapping). This result implies that agricultural land was
not used by cowbirds for feeding, but may also be due to the coarse scale of analysis as
various types of agriculture (i.e. active, fallow, pasture, row crops) are not distinguished by available data. Had we sampled for cowbird presence in the latter half of the day, we may have observed a tighter link between agriculture and detection probability, because cowbirds generally partition the day into nest finding and feeding (e.g. Rothstein et al. 1984). Elsewhere, cowbirds preferred grazed fields, showed a secondary preference for short grass fields, and seldom used ungrazed fields in Missouri (Morris & Thompson 1998) and the Appalachians (Gates & Evans 1998). However, Tewksbury et al. (2006) found no link between parasitism rates and the abundance of agriculture at a landscape scale.

AUTOLOGISTIC REGRESSION MODELS

We had substantial autocorrelation in both our presence/absence data and habitat variables (Fig 2.5). Autocorrelation in residuals of our logistic model indicated that the assumption of independent observations was violated, due either to undescribed environmental variation or intrinsic processes at the population level. However, there are modelling techniques that will help account for spatial autocorrelation, such as autologistic regression for binary data. Using autologistic regression reduced, but did not completely eliminate, the autocorrelation in residuals of our models (Fig. 2.6). Other studies have also found that autocorrelation may still be present in final models, although to a lesser extent than found in non-spatial models (Lichstein et al. 2002; Betts et al. 2006; Wintle & Bardos 2006).

The autologistic model showed some improvement in performance over the logistic and simple models (Table 2.6), and was the only model showing a good fit with the data. The autologistic procedure, in accounting for spatial autocorrelation of errors,
can substantially improve model performance (Augustin et al. 1999; Klute et al. 2002; Lichstein et al. 2002; Priorecky & Prescott 2006) or show smaller improvements in prediction success (Osborne et al. 2001; Betts et al. 2006). Although the magnitude of improvement compared to the standard logistic model seems to differ by case, Wintle & Bardos (2006) found that the autologistic model was robust to a range of sampling designs and intensities. Thus, autologistic regression seems the most appropriate choice for habitat modelling studies using presence/absence data to combat problems of spatial dependencies inherent in these data. In addition, the autologistic model had the most direct link, if the least precise, between model predictions and empirical parasitism rates of hosts.

Modelling the effects of neighboring cells via autologistic regression rendered nearly all of our predictor variables insignificant (Table 2.5). After autocorrelation is incorporated into models, habitat effects often decrease because space and habitat are confounded in the absence of the explicit use of space (Lichstein et al. 2002). Other studies have also found a decrease or loss of significance in predictors and lower parameter estimates in autologistic models (Augustin et al. 1996; Klute et al. 2002; Lichstein et al. 2002).

The inclusion of distance to urban in our models created a strong broad-scale (unidirectional) trend across the study area, but as autologistic regression evaluates autocorrelation in all directions equally, it may not have fully accounted for the spatial pattern in our data. However, we found no consistent pattern when we plotted residuals of the autologistic model against distance to urban, suggesting that the model does control for this element of spatial pattern.
COMPARISON OF LANDSCAPE-SCALE DATASETS

Surprisingly, the best cowbird model with widely available data had only slightly lower performance than the best logistic model. The similarities among all three models were likely a consequence of each containing distance to urban. The differences in the simple model then stemmed from the other two variables included: Landsat landcover and distance to forest, implying cowbirds prefer breeding in forested areas. When both landcover datasets were available for inclusion, models selected the digitized data (EM), suggesting it was more useful to discrimination. In the case of cowbirds, we suspect that, the digitized data available, although perhaps more subject to errors, provided more ecologically meaningful classes and detail than the remote-sensing imagery.

Habitat modelling studies rarely have more than one habitat cover layer available. Landsat imagery is used in 80% of avian habitat studies applying remote-sensing imagery, likely due to wide coverage and public access (Gottschalk et al. 2005). A study comparing the utility of digitized data versus classified remote-sensing data for a landscape-scale wildlife study in Minnesota found that the datasets were more similar than expected, but that the digitized data contained more detail, particularly for underrepresented cover classes (Cunningham 2006). We suggest that digitized data, where available and depending on the manner in which it was classified, may be the best option for local habitat studies, but that satellite imagery data are a suitable and inexpensive alternative for studies over a broader geographic area, exploratory analyses, or when funds limit data acquisition.

Since one of this study's goals is to provide information to managers on which landscape features influence cowbird distribution and parasitism of hosts, the models
created with different datasets differ considerably in interpretation. Our results strongly suggest that distance to urban influences cowbirds, but urban is more difficult to manage for than other land uses. A number of studies have suggested that planning for broad forested expanses may protect songbird hosts from parasitism (e.g. Donovan et al. 1995; Robinson et al. 1995b), as suggested by our simple model. However, as our island landscape is primarily divided into small private landholdings, there is little chance for large protected reserves. Rather, it would be more profitable to focus on managing for cowbird foraging areas, such as the locations of cattle.

**VALIDATION**

Independent validations of models will be critical to land use planning decisions with social and economic consequences because fitted models tend to perform optimistically (see Hosmer & Lemeshow 2000). Assessing model predictions against an independent dataset is also crucial when researchers wish to generalize model predictions to other regions. Betts et al. (2006) found that only half of their species models performed reliably when tested against independent data in a new area (~250km away), and that high predictive power based on training data did not forecast good performance with the testing data. Unfortunately, few studies have attempted to validate habitat models with independent data (but see Thogmartin et al. 2004; Betts et al. 2006), often because those data are costly or unavailable. We used an independent dataset representing the occurrence of brown-headed cowbirds over 8 years via the parasitism rates experienced by one of their most preferred host species in our study area, the song sparrow. Indeed, our model predictions increased linearly with parasitism, validating our
predictions about cowbird occurrence and showing promise for their ability to predict actual impact on hosts.

**MAPPING**

While there is a long history of studies relating species' distributions to their environments, models developed for this purpose have proliferated especially rapidly of late due to their potential application in conservation and an increase in available techniques (Guisan & Zimmermann 2000; Guisan & Thuiller 2005). Although fewer studies have yet taken the extra step to create predictive maps (but see Gibson et al. 2004; Thogmartin et al. 2004; Priorecky & Prescott 2006), advances in mapping techniques and GIS will likely increase the emphasis on map products and precision. We used newer software, the Map Comparison Kit, to assist in map comparison because it provided quantitative, objective, and repeatable results, and has to the potential to facilitate predictive mapping and scenario analysis (Hagen 2003). We suggest that more studies producing maps employ such quantitative assessment as it may improve inference and encourage comparison among studies.

**Conclusions**

Our results suggest that land managers interested in predicting cowbird distribution and their influence on hosts, and modelling other bird-habitat relationships, may achieve those aims in relatively cost-effective ways using publicly available data. We also show that accounting for spatial autocorrelation improved model performance, and that plausible models created with only widely available data were improved by also including more detailed data, and thus these approaches may be superior for management...
purposes. Finally, properly validating and comparing models and maps can improve the evaluation and interpretation of habitat models. In the case of cowbirds, our results identified landscape factors likely to influence cowbird distribution in our region, as well as potential refuges from parasitism in space. Our models have the potential to facilitate land use decisions and scenario analyses aimed at reduced cowbirds impacts for management of host persistence.
Table 2.1: Alternative hypotheses for factors affecting cowbird distribution. Names of the hypotheses, a justification citing relevant prior studies, and the variables used to test them are provided (variables defined in Table 2.2).

<table>
<thead>
<tr>
<th>Name (Abbreviation)</th>
<th>Justification</th>
<th>Variables included</th>
</tr>
</thead>
<tbody>
<tr>
<td>Local Variables (LOCAL)</td>
<td>Variation in cowbird distribution may be due to proximate (local) cues such as host species richness and abundance(^1) and local vegetation structure.(^2)</td>
<td>SUIT + SOSP + CCL</td>
</tr>
<tr>
<td>Distance to Feeding Areas (FEED)</td>
<td>Cowbirds may be more common closer to feeding areas; studies have shown cowbird abundance decreases with distance to agriculture,(^3)(^4) residential areas,(^5) and livestock.(^6)(^7)</td>
<td>DURB + DAG + DCAT + DSUB</td>
</tr>
<tr>
<td>Landscape Context (CONTEXT)</td>
<td>The relative proportion of feeding areas in the landscape (landscape context) may affect cowbird distribution; studies have suggested cowbirds respond to the density of livestock feeding areas,(^8) agriculture,(^9) and suburban/rural.(^10)</td>
<td>PAG + PCAT + PSUB</td>
</tr>
<tr>
<td>Availability of Breeding Habitat (BREED)</td>
<td>Preferences for particular breeding locations may outweigh the need for cowbirds to be near feeding opportunities. Breeding tends to occur in forest(^11) and show a relationship with forest edge.(^12)</td>
<td>DFOR + CCS</td>
</tr>
<tr>
<td>Landcover (COVER)</td>
<td>Cowbirds may also prefer certain landcover classes,(^1)(^3)(^13)(^14) perhaps because they are more likely to find potential hosts in one class than another.</td>
<td>LSAT</td>
</tr>
<tr>
<td>Integrated Landscape (LANDSCAPE)</td>
<td>Although distances to feeding areas are expected to influence cowbird distribution, this may also be confounded by landcover class preferences. Thus, LANDSCAPE is a combination of the FEED and COVER hypotheses.</td>
<td>DURB + DAG + DCAT + DSUB + LSAT</td>
</tr>
<tr>
<td>Global (GLOBAL)</td>
<td>Cowbirds may be responding to all of these above factors, and studies comparing multiple models should include a global model.</td>
<td>DURB + DAG + DCAT + DSUB + PAG + PCAT + PSUB + LSAT + DFOR + SUIT + SOSP + CCL</td>
</tr>
</tbody>
</table>

Table 2.2: Descriptions of predictive variables used in analyses of cowbird occurrence and their parent GIS layer. Context variables are the proportion of the specified landcover type within a 2.5 km radius.

<table>
<thead>
<tr>
<th>Variable Description</th>
<th>Source</th>
<th>Code</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Landcover</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ecosystem Mapping: landcover digitized from orthophotos into 7 classes: Agriculture (AG), Rural (RW), Herbaceous (HB), Wet Habitats (WE), Mature Forest (MF), Woodland (WD), Young Forest (YF)</td>
<td>Islands Trust Ecosystem Mapping</td>
<td>EM</td>
</tr>
<tr>
<td>Landsat landcover classified into 8 classes: Exposed Land, Herb, Shrub, Wetland, Broadleaf, Sparse Coniferous, Open Coniferous, Dense Coniferous</td>
<td>Landsat</td>
<td>LSAT</td>
</tr>
<tr>
<td>Landcover collapsed into forest (≥10% crown closure) vs. nonforest</td>
<td>Landsat-derived</td>
<td>FOR</td>
</tr>
<tr>
<td>Landcover collapsed into 4 levels of crown closure (1=0-10%; 2=10-25%; 3=26-60%; 4=60-100%)</td>
<td>Landsat-derived</td>
<td>CCS</td>
</tr>
<tr>
<td><strong>Landscape: Distance Variables (m)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance to urban</td>
<td>Aerial photos</td>
<td>DURB</td>
</tr>
<tr>
<td>Distance to Vancouver Island</td>
<td>Basemaps</td>
<td>DVI</td>
</tr>
<tr>
<td>Distance to nearest agriculture I</td>
<td>EM-derived, aerial photos</td>
<td>DAG</td>
</tr>
<tr>
<td>Distance to nearest agriculture II</td>
<td>Agricultural Land Reserve</td>
<td>DALR</td>
</tr>
<tr>
<td>Distance to nearest suburban</td>
<td>EM-derived, aerial photos</td>
<td>DSUB</td>
</tr>
<tr>
<td>Distance to nearest forest</td>
<td>Local expertise, field data</td>
<td>DCAT</td>
</tr>
<tr>
<td>Distance to nearest non-forest</td>
<td>Landsat-derived</td>
<td>DFOR</td>
</tr>
<tr>
<td><strong>Landscape: Context Variables</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proportion of agriculture I</td>
<td>EM-derived, aerial photos</td>
<td>PAG</td>
</tr>
<tr>
<td>Proportion of agriculture II</td>
<td>Agricultural Land Reserve</td>
<td>PALR</td>
</tr>
<tr>
<td>Proportion of farms with cattle</td>
<td>Local expertise, Field data</td>
<td>PCAT</td>
</tr>
<tr>
<td>Proportion of suburban</td>
<td>EM-derived, aerial photos</td>
<td>PSUB</td>
</tr>
<tr>
<td>Proportion of forest</td>
<td>Landsat-derived</td>
<td>PFOR</td>
</tr>
<tr>
<td><strong>Local Variables</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percent canopy cover within 100m radius of point count location</td>
<td>Aerial photos</td>
<td>CCL</td>
</tr>
<tr>
<td>Total avian species richness at point count</td>
<td>Field data</td>
<td>RICH</td>
</tr>
<tr>
<td>Richness of suitable cowbird hosts at point count</td>
<td>Field data</td>
<td>SUIT</td>
</tr>
<tr>
<td>Abundance of song sparrows at point count</td>
<td>Field data</td>
<td>SOSP</td>
</tr>
</tbody>
</table>
Table 2.3: Univariate comparisons of local and landscape features at point count sites where brown-headed cowbirds were detected \((n = 135)\) or not \((n = 342)\). All tests employed Mann-Whitney U-statistics, adjusted for multiple comparisons by Bonferroni correction.\(^1\)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Present Mean</th>
<th>SE</th>
<th>Absent Mean</th>
<th>SE</th>
<th>U-test</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>CCL</td>
<td>46.037</td>
<td>2.307</td>
<td>54.082</td>
<td>1.427</td>
<td>27162.0</td>
<td>0.002**</td>
</tr>
<tr>
<td>CCS</td>
<td>2.022</td>
<td>0.094</td>
<td>2.228</td>
<td>0.057</td>
<td>25484.5</td>
<td>0.057</td>
</tr>
<tr>
<td>SOSP</td>
<td>1.837</td>
<td>0.122</td>
<td>1.366</td>
<td>0.080</td>
<td>18068.0</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>RICH</td>
<td>9.215</td>
<td>0.250</td>
<td>7.333</td>
<td>0.142</td>
<td>14499.5</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>SUIT</td>
<td>4.956</td>
<td>0.194</td>
<td>4.474</td>
<td>0.116</td>
<td>19928.0</td>
<td>0.019*</td>
</tr>
<tr>
<td>DFOR</td>
<td>24.117</td>
<td>5.496</td>
<td>29.787</td>
<td>5.399</td>
<td>20299.5</td>
<td>0.021*</td>
</tr>
<tr>
<td>DNFOR</td>
<td>40.364</td>
<td>5.303</td>
<td>60.687</td>
<td>4.195</td>
<td>26854.5</td>
<td>0.004*</td>
</tr>
<tr>
<td>DVI</td>
<td>7495.78</td>
<td>606.6</td>
<td>10703.6</td>
<td>369.1</td>
<td>30313.5</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>DURB</td>
<td>9429.3</td>
<td>694.6</td>
<td>14346.2</td>
<td>418.6</td>
<td>31667.5</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>DCAT</td>
<td>2292.2</td>
<td>235.0</td>
<td>2920.4</td>
<td>183.1</td>
<td>24542.5</td>
<td>0.282</td>
</tr>
<tr>
<td>DAG</td>
<td>1284.5</td>
<td>107.4</td>
<td>1076.1</td>
<td>76.0</td>
<td>19118.0</td>
<td>0.003**</td>
</tr>
<tr>
<td>DSUB</td>
<td>3449.2</td>
<td>200.4</td>
<td>3770.0</td>
<td>141.0</td>
<td>23504.0</td>
<td>0.757</td>
</tr>
<tr>
<td>PAG</td>
<td>0.0180</td>
<td>0.002</td>
<td>0.032</td>
<td>0.002</td>
<td>27679.5</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>PCAT</td>
<td>0.021</td>
<td>0.002</td>
<td>0.017</td>
<td>0.001</td>
<td>19969.5</td>
<td>0.018*</td>
</tr>
<tr>
<td>PSUB</td>
<td>0.006</td>
<td>0.001</td>
<td>0.003</td>
<td>&lt;0.001</td>
<td>19642.5</td>
<td>0.006*</td>
</tr>
<tr>
<td>PFOR</td>
<td>0.219</td>
<td>0.016</td>
<td>0.308</td>
<td>0.011</td>
<td>29583.5</td>
<td>&lt;0.001**</td>
</tr>
</tbody>
</table>

\(^1\) Significant at \(\alpha=0.05\) (*) or after Bonferroni correction \(\alpha^*=0.05/16=0.003\) (**)
Table 2.4: Comparison of a priori models relating cowbird occurrence to landscape features \((n = 477)\). See Table 2.1 for descriptions of hypotheses.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>(K^1)</th>
<th>(\Delta AIC)</th>
<th>(R^2)</th>
<th>AUC</th>
</tr>
</thead>
<tbody>
<tr>
<td>LOCAL</td>
<td>4</td>
<td>62.99</td>
<td>0.084</td>
<td>0.659</td>
</tr>
<tr>
<td>FEED</td>
<td>5</td>
<td>40.03</td>
<td>0.153</td>
<td>0.706</td>
</tr>
<tr>
<td>CONTEXT</td>
<td>4</td>
<td>47.84</td>
<td>0.126</td>
<td>0.709</td>
</tr>
<tr>
<td>BREED</td>
<td>3</td>
<td>83.35</td>
<td>0.019</td>
<td>0.569</td>
</tr>
<tr>
<td>COVER</td>
<td>2</td>
<td>62.59</td>
<td>0.074</td>
<td>0.618</td>
</tr>
<tr>
<td>LANDSCAPE</td>
<td>6</td>
<td>23.04</td>
<td>0.203</td>
<td>0.734</td>
</tr>
<tr>
<td>GLOBAL</td>
<td>13</td>
<td>0</td>
<td>0.295</td>
<td>0.793</td>
</tr>
</tbody>
</table>

\(^1\) Number of variables including intercept
Table 2.5: Variable parameters for best logistic and autologistic models of cowbird occurrence.

<table>
<thead>
<tr>
<th>Variable</th>
<th>B</th>
<th>SE</th>
<th>P</th>
<th>\text{Exp}(\beta)</th>
<th>\text{Upper} 95% CI</th>
<th>\text{Lower} 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Best logistic model</strong></td>
<td></td>
<td></td>
<td></td>
<td>Odds Ratio</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>-2.064</td>
<td>0.948</td>
<td>0.030</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>DURB</td>
<td>-0.021</td>
<td>0.004</td>
<td>&lt;0.001</td>
<td>0.979</td>
<td>0.986</td>
<td>0.972</td>
</tr>
<tr>
<td>EM(^1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AG</td>
<td>3.134</td>
<td>0.778</td>
<td>&lt;0.001</td>
<td>22.955</td>
<td>105.422</td>
<td>4.998</td>
</tr>
<tr>
<td>HB</td>
<td>-0.232</td>
<td>0.356</td>
<td>0.515</td>
<td>0.793</td>
<td>1.594</td>
<td>0.394</td>
</tr>
<tr>
<td>MF</td>
<td>-1.222</td>
<td>0.769</td>
<td>0.112</td>
<td>0.295</td>
<td>1.331</td>
<td>0.065</td>
</tr>
<tr>
<td>RW</td>
<td>1.195</td>
<td>0.413</td>
<td>0.004</td>
<td>3.304</td>
<td>7.424</td>
<td>1.471</td>
</tr>
<tr>
<td>WD</td>
<td>-0.667</td>
<td>0.427</td>
<td>0.118</td>
<td>0.513</td>
<td>1.185</td>
<td>0.222</td>
</tr>
<tr>
<td>WE</td>
<td>1.568</td>
<td>0.605</td>
<td>0.010</td>
<td>4.796</td>
<td>15.687</td>
<td>1.467</td>
</tr>
<tr>
<td>DAG</td>
<td>0.414</td>
<td>0.120</td>
<td>&lt;0.001</td>
<td>1.513</td>
<td>1.914</td>
<td>1.196</td>
</tr>
<tr>
<td>PCAT</td>
<td>4.731</td>
<td>1.565</td>
<td>0.003</td>
<td>113.380</td>
<td>2436.311</td>
<td>5.276</td>
</tr>
<tr>
<td><strong>Best autologistic model (1200m)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>-3.639</td>
<td>1.038</td>
<td>&lt;0.001</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>DURB</td>
<td>-0.007</td>
<td>0.005</td>
<td>0.226</td>
<td>0.994</td>
<td>1.004</td>
<td>0.983</td>
</tr>
<tr>
<td>EM(^1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AG</td>
<td>2.434</td>
<td>0.781</td>
<td>0.002</td>
<td>11.403</td>
<td>52.743</td>
<td>2.465</td>
</tr>
<tr>
<td>HB</td>
<td>0.469</td>
<td>0.408</td>
<td>0.250</td>
<td>1.599</td>
<td>3.558</td>
<td>0.719</td>
</tr>
<tr>
<td>MF</td>
<td>-0.555</td>
<td>0.789</td>
<td>0.482</td>
<td>0.574</td>
<td>2.699</td>
<td>0.122</td>
</tr>
<tr>
<td>RW</td>
<td>1.103</td>
<td>0.422</td>
<td>0.009</td>
<td>3.015</td>
<td>6.894</td>
<td>1.318</td>
</tr>
<tr>
<td>WD</td>
<td>0.263</td>
<td>0.486</td>
<td>0.588</td>
<td>1.301</td>
<td>3.375</td>
<td>0.502</td>
</tr>
<tr>
<td>WE</td>
<td>1.241</td>
<td>0.627</td>
<td>0.048</td>
<td>3.460</td>
<td>11.82</td>
<td>1.012</td>
</tr>
<tr>
<td>DAG</td>
<td>0.220</td>
<td>0.126</td>
<td>0.081</td>
<td>1.247</td>
<td>1.596</td>
<td>0.974</td>
</tr>
<tr>
<td>PCAT</td>
<td>2.423</td>
<td>1.707</td>
<td>0.156</td>
<td>11.279</td>
<td>320.235</td>
<td>0.397</td>
</tr>
<tr>
<td>Autocovariate</td>
<td>0.033</td>
<td>0.009</td>
<td>&lt;0.001</td>
<td>1.033</td>
<td>1.052</td>
<td>1.015</td>
</tr>
</tbody>
</table>

\(^1\) Reference class for EM categorical variable is YF (Young Forest)
Table 2.6: Model evaluation of the three final ‘best’ cowbird models \((n = 477)\), including bootstrap-adjusted performance statistics with percent change in parentheses \((n = 1000)\).

<table>
<thead>
<tr>
<th>Model</th>
<th>(K)</th>
<th>(\Delta AIC)</th>
<th>(R^2)</th>
<th>AUC</th>
<th>(R^2_{corr})</th>
<th>(AUC_{corr})</th>
<th>Emax</th>
</tr>
</thead>
<tbody>
<tr>
<td>Logistic</td>
<td>5</td>
<td>11.80</td>
<td>0.242</td>
<td>0.767</td>
<td>0.196 (19.0%)</td>
<td>0.748 (2.5%)</td>
<td>0.047</td>
</tr>
<tr>
<td>Simple</td>
<td>4</td>
<td>24.49</td>
<td>0.207</td>
<td>0.743</td>
<td>0.155 (25.1%)</td>
<td>0.721 (3.0%)</td>
<td>0.056</td>
</tr>
<tr>
<td>Autologistic</td>
<td>6</td>
<td>0</td>
<td>0.276</td>
<td>0.777</td>
<td>0.228 (17.4%)</td>
<td>0.758 (2.4%)</td>
<td>0.044</td>
</tr>
</tbody>
</table>

\(^1\) Number of variables including intercept
Table 2.7: Parameters for the best simple model of cowbird occurrence.

<table>
<thead>
<tr>
<th>Variable</th>
<th>B</th>
<th>SE</th>
<th>P</th>
<th>Exp(β) Odds Ratio</th>
<th>Upper 95% CI</th>
<th>Lower 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>0.986</td>
<td>0.360</td>
<td>0.006</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>DURB</td>
<td>-0.021</td>
<td>0.003</td>
<td>&lt;0.001</td>
<td>0.979</td>
<td>0.986</td>
<td>0.973</td>
</tr>
<tr>
<td>LSAT&lt;sup&gt;1&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EXPOSED</td>
<td>2.401</td>
<td>0.583</td>
<td>&lt;0.001</td>
<td>11.032</td>
<td>34.555</td>
<td>3.522</td>
</tr>
<tr>
<td>HERB</td>
<td>1.211</td>
<td>0.508</td>
<td>0.017</td>
<td>3.357</td>
<td>9.085</td>
<td>1.241</td>
</tr>
<tr>
<td>SHRUB</td>
<td>2.265</td>
<td>0.651</td>
<td>0.0005</td>
<td>9.630</td>
<td>34.497</td>
<td>2.688</td>
</tr>
<tr>
<td>WETLAND</td>
<td>2.745</td>
<td>1.551</td>
<td>0.077</td>
<td>15.572</td>
<td>325.717</td>
<td>0.744</td>
</tr>
<tr>
<td>DECIDUOUS</td>
<td>-0.0003</td>
<td>0.537</td>
<td>0.999</td>
<td>0.999</td>
<td>2.866</td>
<td>0.349</td>
</tr>
<tr>
<td>CONIFER-D&lt;sup&gt;2&lt;/sup&gt;</td>
<td>0.545</td>
<td>0.595</td>
<td>0.359</td>
<td>1.725</td>
<td>5.534</td>
<td>0.538</td>
</tr>
<tr>
<td>CONIFER-S&lt;sup&gt;2&lt;/sup&gt;</td>
<td>-0.248</td>
<td>0.421</td>
<td>0.556</td>
<td>0.780</td>
<td>1.781</td>
<td>0.342</td>
</tr>
<tr>
<td>DFOR</td>
<td>-0.392</td>
<td>0.131</td>
<td>0.003</td>
<td>0.676</td>
<td>0.873</td>
<td>0.523</td>
</tr>
</tbody>
</table>

<sup>1</sup> Reference LANDSAT category is CONIFER-O<sup>2</sup>

<sup>2</sup> LANDSAT CONIFER is split into 3 sub-groups: D=dense, O=open, S=sparse
Figure 2.1: Location of the study area and point count locations (solid circles). The Southern Gulf Islands are on the border between BC, Canada (shaded) and Washington State, U.S.A. (striped).
Figure 2.2: Predicted probability of cowbird occurrence from best logistic model.
Figure 2.3: Predicted probability of cowbird occurrence from best autologistic model.
Figure 2.4: Predicted probability of cowbird occurrence from best simple model.
Figure 2.5: Moran’s $I$ correlograms for (a) raw data and (b-e) variables selected by best models. $I$ has an expected value near zero for no spatial autocorrelation, with negative and positive values indicating positive and negative autocorrelation, respectively. Closed circles represent values that are significantly different from the null hypothesis of no autocorrelation (one-tailed test, using $\alpha=0.05$ with a progressive Bonferroni’s correction); open circles are not significant.
Figure 2.6: Moran's $I$ correlograms for residuals of the three final models of cowbird occurrence.
Figure 2.7: Performance of model relative to independent data. Average parasitism rates in relation to mean predicted probability of occurrence on 12 islands within the study area. The figure includes data and regression lines for the best logistic (circles, dashed line), autologistic (triangles, solid line), and simple (squares, dotted line) models.
References


CHAPTER 3: 
CONSEQUENCES OF PARASITE INVASION AND LAND USE ON THE 
DEMOGRAPHY OF ISLAND POPULATIONS OF HOSTS

Introduction

The occurrence of source-sink dynamics can have huge consequences for the ecology and conservation of species (see Kawecki 2004). Where source-sink dynamics occur, some populations cannot produce enough recruits to sustain themselves (sinks), and thus rely on immigrants from more productive (source) populations; the differences between them are thought to result mainly via habitat-specific variation in survival and fecundity (Pulliam 1988). Thus, to predict the regional dynamics of natural populations and identify effective conservation strategies, we must first understand the basis of spatial variation in population viability (Pulliam & Danielson 1991; Donovan et al. 1995b).

Spatial heterogeneity in habitat structure and demography has often been used to predict species’ distributions and identify critical habitat, but less frequently to predict the spatial dynamics of populations. For example, the effects of habitat quality and change on the population structure (e.g. Fryxell 2001; Reid et al. 2006) or population viability (e.g. Akcakaya 2000; Akcakaya et al. 2004; Larson et al. 2004; Schumaker et al. 2004) of single species have been extensively modeled. Several studies have also examined the coexistence of species and their competitor, predator or parasite enemies in a theoretical framework (e.g. May & Robinson 1985; Namba et al. 1999; Barabás et al. 2004) or by estimating the effects of enemies on spatial dynamics using habitat fragmentation as a surrogate (Temple & Cary 1988; Donovan et al. 1995a; With & King 2001; Lloyd et al.

2 A version of this chapter will be submitted for publication. Jewell, K.J. and Arcese, P. Consequences of parasite invasion and land use on the demography of island populations of hosts.
2005). It remains to be shown, however, that empirical relationships of enemy abundance, habitat type and demographic rate can used to predict population trends, and that those predictions can be validated by comparison with censuses of regional population trend.

Here, we present empirical data and a spatial model to describe the spatial demography of an archetypical passerine, the song sparrow *Melospiza melodia*, in relation to its main enemy, the brown-headed cowbird *Molothrus ater*. Specifically, we predicted and mapped expected population growth rates ($\lambda$) for sparrows in the Southern Gulf Islands, BC, Canada (SGI), using data from 17 populations studied intensively for 1-36 years from 1960 to 2006, and experiencing varying levels of parasitism by cowbirds. We also validated our predictions of population growth rate by comparison to local and regional censuses and population trend.

We modelled the consequences of parasitism for a host based on strong evidence that cowbirds control song sparrow demography via their effects on fecundity (Smith et al. 2002; Smith et al. 2006a). Cowbirds are brood parasites implicated in the decline of many host species (Mayfield 1977), mainly via their effects on host reproductive rate (i.e. Robinson et al. 1995; Kus & Whitfield 2005), and particularly where they have invaded new habitats and regions as a consequence of land conversion (Rothstein 1994). However, several studies of song sparrows, a preferred cowbird host (Lowther 1993; Scott & Lemon 1996), suggest that cowbird impacts on host demography have been underestimated. On Mandarte Island, where song sparrows have been studied intensively for 36 years, Smith et al. (2006a) concluded that cowbirds can limit population growth, mainly via their effects on the rate of nest failure. High parasitism rates (~60-80%)
among song sparrows in the Fraser River delta of mainland BC led to the development of population sinks (Smith et al. 1996; Rogers et al. 1997); but these became self-sustaining ($\lambda > 1$) when cowbirds, parasitism, and nest failure were experimentally reduced (Smith et al. 2002). Because cowbirds only invaded coastal BC in the 1950s (Peterjohn et al. 2000), they pose a relatively new threat to potential hosts in the region. However, because cowbird distribution and abundance is closely tied to the distribution of potential feeding areas (see Chapter 2; reviewed in Chace et al. 2005), it is likely that source-sink dynamics develop as a consequence of spatial variation in the intensity of parasitism (Wilson & Arcese 2006).

Two main questions drove this study. First, we asked if spatial limits on cowbird distribution create refugia for host populations. We next asked if we could predict the regional effect of cowbirds on a common host. Based on prior knowledge, we hypothesized that sparrow populations further from cowbird feeding areas may provide a refuge from parasitism and experience higher reproductive rates than in populations with abundant cowbirds. We used field surveys, geographical information systems (GIS), and species habitat and population models to (1) predict potential parasitism rates based on landscape features influencing cowbird distribution; (2) identify the potential distribution of song sparrows; (3) relate song sparrow reproductive output to cowbird parasitism rates; and (4) map potential population growth rates for song sparrows considering the impact of parasitism.
Materials and Methods

STUDY AREA

We studied cowbirds and song sparrows in the Southern Gulf Islands (SGI), located in the Strait of Georgia between Vancouver Island (VI) and the mainland of British Columbia, Canada. The area has a mild Mediterranean climate due to the protection of the Olympic and Vancouver Island mountains. Vegetation falls predominately into the Coastal Douglas Fir *Pseudotsuga menziesii* biogeoclimatic zone. Many smaller islands are vegetated by sea island scrub. Our study area was the southern portion of the SGI, measuring approximately 27 x 57 km (123°00’ W, 48°32’ N; Fig. 3.1). Elevation ranges from 0-600m a.s.l. The study area includes over 100 islands, ranging in size from tiny islets to 186 km²; in total they comprise roughly 380 km². The study area is about 70% forested, 13% rural, 6% agriculture, 2% suburban, and 9% other (Islands Trust Ecosystem Mapping Project). The area also includes the Southern Gulf Island National Park, protecting over 35 km² across 15 islands.

STUDY SPECIES

*Song sparrow*—Song sparrows occur broadly throughout North America, generally inhabiting early-successional habitats near water. In our study area, song sparrows are abundant in sea island scrub (Arcese et al. 1992) and dry forest (Smith et al. 1996). Nests are typically located in shrubs. Many song sparrow populations are migratory, but along coastal British Columbia, they are year-round residents (Tompa 1964; Arcese et al. 2002). They are highly territorial (Arcese 1989b) and philopatric (Arcese 1989a). Territory sizes range widely, primarily determined by conspecific population density (Arcese et al. 2002). On Mandarte Island, for example, territories range from under
200m² to 5,000m² (Arcese 1989a). Song sparrows are relatively short-lived, generally reproducing from 1 to 4 years (Arcese et al. 2002). In coastal BC, song sparrows nest from March to July, and are capable of raising up to four broods in a year (Smith et al. 2006d). They seem to tolerate moderate levels of parasitism because they are able to rear both cowbird and their own young successfully and early season nests often escape parasitism due to the length of the sparrows’ breeding season (Smith 1981; Smith & Arcese 1994).

Brown-headed cowbird- Cowbirds search for hosts in forest, marsh and shrubland, but feed in short grass pastures and lawns (Rothstein et al. 1984; Thompson 1994; Chace et al. 2003). The commuting distance to foraging areas restricts cowbirds’ use of potential breeding sites (e.g. Tewksbury et al. 1999; Goguen & Mathews 2001), thus there is spatial variation in the parasitism of hosts (e.g. Smith & Myers-Smith 1998; Wilson & Arcese 2006). Cowbirds affect host species through the removal of host eggs (Sealy 1992), abandonment of parasitized nests (Budnik et al. 2001), interspecific nestling competition (Hauber 2003), and predation on nests (Arcese et al. 1996; Arcese & Smith 1999). On Mandarte, cowbirds reduced the reproductive success of sparrows by reducing the number of young fledged per nest and by increasing nest failure rate (Smith et al. 2006c).

SPECIES DISTRIBUTION MODELS

Surveys- We developed species distribution models for brown-headed cowbirds and song sparrows from occurrence data drawn from 531 avian point counts conducted on 35 different islands between 6 May and 10 July 2005. One to two trained observers conducted these single-visit counts between 0600 and 1100 hrs. We recorded distances
from the observer to each bird up to 100 m. After each count, we played a locally-
recorded song from a male song sparrow four times, each facing in a different direction,
paused one minute, and then repeated the playbacks. Playbacks allowed us to more
accurately assess the occurrence of song sparrows and effectively widened our count
duration to 13 minutes. We used all data (up to 100 m distance and including birds
detected from playbacks) in order to increase our power to detect differences between
occupied and unoccupied sites. We stratified the location of counts in order to include
all landcover classes available in GIS layers, aiming to separate counts by at least 200 m.
Point count locations were recorded using a handheld GPS device (GPS60, Garmin Ltd,
Kansas, USA). More details about our survey procedure can be found in Chapter 2.

Habitat models- Our species distribution model for the brown-headed cowbird is
taken from Chapter 2. In brief, we formed an a priori list of candidate predictor variables
based on their importance to cowbirds and their availability as GIS layers. Our resulting
candidate variables represented vegetation cover and the distance to and proportion of
potential feeding areas and forested areas in the landscape. We created a ‘best’ cowbird
distribution model using an interactive forward stepwise procedure entering variables
with the lowest significance values for their score statistics until the cutoff of \( P = 0.10 \)
(SYSTAT 11.0, SYSTAT Software Inc, San Jose, CA). To avoid collinearity, candidate
variables correlated (\( r_s \geq 0.60 \)) with variables already entered were not allowed in the
model. Because our occurrence and environmental data showed positive spatial
autocorrelation, we corrected for the lack of independence by using autologistic
regression with a modified Gibbs sampler (following Augustin et al. 1996). Using the
best species distribution model from logistic regression, we added on an extra term, the
autocovariate, which modifies the response (predicted probability of occurrence) in a cell based on the probabilities of neighboring cells. Previous studies have shown that the effect of environmental variables is overestimated when spatial autocorrelation is not properly accounted for in statistical models of species distributions; moreover, autologistic models often have more predictive power than standard logistic models (Osborne et al. 2001; Klute et al. 2002; Lichstein et al. 2002; Betts et al. 2006). We chose a spatial neighborhood with a 1,200m radius as the appropriate scale for the autocovariate by comparing a series of models with different neighborhood (clique) sizes using AIC scores (after Burnham & Anderson 2002). More details on the species distribution modeling process can be found in Chapter 2.

Two statistics were used to evaluate the species distribution models: variance explained was assessed using Nagelkerke’s $R^2$ index, which approximates the $R^2$ of least squares regression models (Nagelkerke 1991; Hosmer & Lemeshow 2000), and the models’ discrimination power was assessed using receiver operating characteristics (ROC) plots. ROC plots are increasingly used by ecologists in recognition that model evaluation based on an arbitrary cut-off of predicted probability > 0.5 is often not ecologically suitable (i.e. Fielding & Bell 1997; Gibson et al. 2004). The area under the curve (AUC) of the ROC plot indicates overall fit of the model and varies from 0.5 (no better than chance) to 1.0 (perfect discrimination).

We used the same procedure to model song sparrow distribution; candidate variables were selected based on prior understanding and their availability (Table 3.1). Predictive distribution maps were created for both song sparrows and cowbirds by projecting the autologistic models as a combination of input layers in a raster GIS with a...
25m resolution. The resulting maps estimate the probability that each species occurs in a given pixel.

We incorporated our song sparrow predictive distribution map in our predictions about population performance by assuming that sparrows were present in all cells where probability of occurrence exceeded 0.70. We chose this cut-off because it represented the prevalence of song sparrows in our avian point counts (0.701) and satisfied equality of sensitivity (rate of true positives) and specificity (rate of true negatives) of predictions (0.693, calculated from the ROC curve). Both of these methods are suggested as biologically meaningful ways to devise cut-off points by Lui (2005).

CREATING A PARASITISM MAP

Field data- We used our map of predicted cowbird distribution to create a map of predicted parasitism rate using empirical data on cowbird parasitism of song sparrows on 13 islands in our study area and three mainland sites monitored for 1-8 years from 1995 to 2005 (Table 3.2) throughout the breeding season from March to August. Song sparrows were individually marked with a numbered aluminum band and colored plastic bands. Territories were visited c. weekly to note behavior and locate nests. All nests were found in most of these sites; for each nest we estimated the date of first egg, clutch size, the number of cowbird eggs present, and the number of young fledged. The overall parasitism rate for each site was defined as the number of parasitized song sparrow nests divided by the total number of nests in the season. Some results and more details on methods can be found in Smith et al. (2002; 2006a) and Wilson & Arcese (2006). Although some population data goes back ten years, cowbird abundance seems to have remained constant during this period (M. Taitt, pers. comm; our obs.)
To create our predictive model of parasitism we conducted repeated point counts (50 m radius, 10-min) at each site from May to June of 2005 (islands) and 2006 (subset of seven islands, mainland). For all sites with five or more counts, we estimated cowbird occurrence as the average of all point counts per site (mean: 15.9 ± 1.6, range: 6 – 27; Table 3.2).

Statistical analyses - We used analysis of variance (ANOVA) to estimate the average rate of parasitism experienced by song sparrows at each site, while controlling statistically for the length of the breeding season at each site (date of first-initiated minus last-initiated nest). Parasitism was arcsine-square root transformed to approximate a normal distribution, and then weighted by the square root of the number of nests on which the estimate was based to reduce the influence of estimation error in subsequent analyses (Gilbert 1979; Arcese et al. 1992).

We used simple regression to estimate the relationship between observed probability of occurrence of cowbirds and average parasitism rate experienced by song sparrows in our 15 study sites after transforming these variables to normalize their distributions and forcing the regression through the origin, because parasitism cannot occur if cowbirds are absent. We next used this regression to transform our cowbird distribution map into a predictive map of the expected rate of parasitism rate experienced by song sparrows throughout our study area.

ESTIMATING REPRODUCTIVE OUTPUT

We estimated reproductive output based on the expected rate of parasitism at each map point, and then combined those estimates with empirical data on juvenile and adult survival to estimate the finite rate of population growth (λ). Modelling the effect of
parasitism via seasonal fecundity is more appropriate than nest success or failure because the former captures parasitism’s effect on the nesting cycle as well as reproductive output (Grzybowski & Pease 2000). To estimate reproductive output under parasitism we first used 34 years of detailed data from Mandarte Island to find the most parsimonious model for annual reproductive rate following Arcese and Marr (2006). We then fit that model to our multi-island data using a general linear mixed model in order to estimate reproduction across 10 sites where we made repeated observations of parasitism in two or more years, using ‘island’ as a random factor and an autoregressive covariance structure (Table 3.3; PROC MIXED, SAS 9.0, SAS Institute Inc., Cary, NC). We estimated the total number of fledglings produced in island populations annually using three fixed effects: parasitism, the date on which breeding first commenced in each population (‘date of first egg’, DFE), and total number of females breeding locally. Because cowbirds generally begin breeding in early May, but song sparrows may begin breeding in March to April, earlier DFEs result in a higher fraction of nests escaping parasitism annually and higher reproductive rates on average (Smith & Arcese 1994; Smith et al. 2006c). In the absence of parasitism, reproductive output increased linearly with the number of females breeding from 1960-63 and 1975-2006 on Mandarte Is., but fledgling production was reduced as female numbers increased in years when cowbirds were present (Arcese & Marr 2006; unpubl. res.) due mainly to the effects of cowbirds on nest failure (Arcese et al. 1996; Smith et al. 2006c). Thus, our final model to predict the number of locally-produced fledglings (transformed by log_{10}) used observed parasitism rate, DFE (each untransformed and about normally distributed), and the number of breeding females (transformed by log_{10}).
We used our final model to estimate reproductive output in each pixel of the study area while holding the covariates constant. Thus, assuming that populations would not vary in the onset of breeding, we used the mean value of DFE (Julian date, mean: 103.88 ± 1.34, range: 79 - 126, n = 60). We also assumed that each pixel had an equal population size across the study area, so we estimated the median territory size from Mandarte over 31 years (357.26 m², range: 35.39 - 5067.73, n = 1218 males). According to median density, there should be about 2 females in a 25 m pixel (625 m²). These values were used as our parameters in the final model together with the predictions from our parasitism map.

ESTIMATING POPULATION GROWTH RATE

Our final step was to estimate population growth rate (λ) for song sparrows. We used the equation:

\[ \lambda = S_f + (N_j \times S_j) \]  

Eqn. 3.1

where \( S_f \) = annual survival of breeding females, \( N_j \) = number of female fledglings produced per female, assuming that, on average, there is a 1:1 sex ratio of female : male offspring, and \( S_j \) = survival of fledglings from leaving the nest to breeding age (1 yr). For \( N_j \), we used the output from our reproductive output model (divided by four to get female fledglings produced by each breeding female). A value of \( \lambda = 1.0 \) indicates a stable population, while \( \lambda < 1.0 \) indicates a decreasing population where the death rate surpasses the local production of juveniles, and \( \lambda > 1.0 \) indicates an increasing population.

The survival rate of adult female sparrows, \( S_f = 0.500 \pm 0.316 \) (median ± SD, range: 0 - 1.00, n = 59), was estimated from empirical data on 10 islands studied from 2-8 years (see Table 3.3). Empirical estimates of juvenile survival were extremely low.
(median: 0.000, mean: 0.050, range: 0 - 0.681, n = 59), so instead we assumed that juvenile survival was 50% of adult survival, or \( S_j = 0.250 \), as previously hypothesized for north-temperate passerines (Greenberg 1980; Lloyd et al. 2005). We evaluated the sensitivity of expected \( \lambda \) to variation in adult and juvenile survival rates as well as the strength of the effect of parasitism on reproductive output using natural variation around each estimate. We validated our predictions by comparing them to independent estimates of \( \lambda \) derived from (1) empirical data on reproductive output and survival of local populations annually, (2) empirical trends from census data on populations within the study area, and (3) regional trend estimates from Breeding Bird Survey (BBS) routes\(^3\) within 100-km of the centre of the study area.

**Results**

**MODELLING DISTRIBUTION AND PARASITISM**

Our habitat modelling results suggested that cowbirds preferred to be closer to urban areas, further from agriculture, in areas with more cattle, and some landcover types over others. The parameters for the final autologistic model for cowbird occurrence were (from Chapter 2):

\[
Y = -3.639 - 0.007 \text{[DURB]} + 2.434 \text{[EM_agricult]} + 0.469 \text{[EM_herbaceous]} - 0.555 \\
[\text{EM_maturefor}] + 1.103 \text{[EM_rural]} + 0.263 \text{[EM_woodland]} + 1.241 \text{[EM_wethabitat]} + \\
0.220 \text{[DAG]} + 2.423 \text{[PCAT]} + 0.033 \text{[AUTOCOV]} \quad \text{Eqn. 3.2}
\]

Descriptions of the variables can be found in Table 3.1. The cowbird model described a moderate amount of the variance in cowbird occurrence (Nagelkerke \( R^2 = 0.276 \)) and

\(^3\) [http://www.mbr pwrc.usgs.gov/bbs/bbs.html]
showed high discrimination between occupied and unoccupied sites (AUC = 0.777; Fig. 2.3).

The song sparrow modelling indicated that song sparrows preferred to be closer to the ocean, further from fresh water, in sparser forests, and in areas with a high heterogeneity of landcover types (see Appendices 2 - 4). The best autologistic model for song sparrows used a spatial neighborhood with a 1200 m radius (see Appendices 1 & 4). The song sparrow model was similar but slightly less successful than the cowbird model in explaining variance (Nagelkerke $R^2 = 0.237$) and discrimination (AUC = 0.748). The parameters for the final autologistic model of song sparrow occurrence are:

$$Y = -0.203 + 0.961 \text{[EM_agricult]} + 0.329 \text{[EM_herbaceous]} - 0.399 \text{[EM_maturefor]} + 0.701 \text{[EM_rural]} - 0.312 \text{[EM_woodland]} + 15.477 \text{[EM_wethabitat]} - 0.328 \text{[DOC]} + 0.192 \text{[HET1]} + 0.008 \text{[DWAT]} - 0.464 \text{[CCS_1]} - 0.438 \text{[CCS_2]} - 0.867 \text{[CCS_3]} + 0.029 \text{[AUTOCOV]}$$

Eqn. 3.3

Based on our cut-off of 0.70 probability of sparrow occurrence, song sparrows were predicted to occur in 50% (191 km$^2$) of our landscape.

Parasitism rates observed annually across all sites varied from 0 to 0.81 of all nests initiated (mean: $0.319 \pm 0.027, n = 83$). The frequency of parasitism differed among sites, with site and season length accounting for 79% of the total variance observed (ANOVA: ‘island’: $F_{15,66} = 16.74, P < 0.001$; ‘season length’: $F_{1,66} = 10.45, P = 0.002$). Least-squared mean estimates for the expected rate of parasitism in each site increased about linearly with the observed probability of observing cowbirds in point counts ($r^2 = 0.87, \text{SEE} = 0.23, F_{1,14} = 97.29, P < 0.001$; Fig. 3.2). We used the slope of
this regression equation, $\beta = 0.828$, to transform our cowbird distribution map into a map of expected parasitism rates of song sparrows (Fig. 3.3).

Predicted parasitism rates from our map ranged from 0 to 0.79, and were higher in those regions where song sparrows were predicted to occur (mean: $0.182 \pm 0.139$ SD) in comparison to the entire landscape (mean: $0.152 \pm 0.121$ SD). Spatially, high and moderate levels of parasitism were concentrated in a belt across the center of the study area, running roughly southwest to northeast (Fig. 3.3). Observed parasitism rates at sites with low probabilities of cowbird occurrence tended to be lower than expected (Fig. 3.2).

**REPRODUCTIVE OUTPUT**

Our mixed model showed that parasitism contributed significantly to reproductive output ($t = -2.37, P = 0.022$; ‘DFE’: $t = -4.38, P < 0.001$; ‘females’: $t = 10.00, P < 0.001$). The mixed model was significantly different than a null model ($\chi^2 = 6.16, df = 1, P = 0.013$), and likelihood ratio tests indicated that our random factor (‘island’) should be kept in the model ($\chi^2 = 3.9, df = 1, P < 0.05$). The resulting parameter estimates were:

$$Y = 1.777 + 0.902 \log(\text{females}) - 0.010 \text{DFE} - 0.308 \text{parasitism}$$

The resulting map predicts that song sparrow populations will produce 4.60 young per female in the absence of parasitism, and 2.42 young per female where parasitism is highest (mean: $4.02 \pm 0.41$ SD). These results correspond well with the mean reproductive success from Mandarte ($4.01 \pm 0.27, n = 31$ years) and all islands ($3.95 \pm 0.28, n = 60$ island-years).

**PREDICTED POPULATION GROWTH RATES**

Based on the mean predicted $\lambda$, the population trend is expected to be stable overall, with a number of strong sinks where parasitism is expected to be high, and no
strong sources (Fig. 3.4; mean $\lambda$: 1.002 $\pm$ 0.052 SD, range: 0.803 – 1.076). Thus, the population growth rate was positive in the absence of parasitism, but negative when the parasitism rate reached 20%. However, including only the portion of the study area from which the demographic data is drawn (about 27 km²; see Fig. 3.1), the population trend is expected to be decreasing at a rate of 8% per annum (mean $\lambda$: 0.922 $\pm$ 0.056 SD, range: 0.803 – 1.066).

Population growth rates were very sensitive to changes in adult and juvenile survival estimates (Fig. 3.5). At the mean predicted parasitism rate in the landscape (0.18), varying either adult or juvenile survival (by 1 SD) had the same effect (32% change each). However, varying juvenile survival had a greater effect at low predicted parasitism rates than at higher rates (Fig. 3.5b). In contrast, varying the strength of the effect of parasitism on reproductive output had less of an effect on $\lambda$ (Fig. 3.5c), changing 4% at the mean parasitism rate, but 10% at the maximum parasitism rate (0.80).

Observed annual values of $\lambda$ on 10 islands studied from 2-8 years (see Table 3.3) averaged $0.959 \pm 0.070$ SE (range: 0 – 2.36, $n = 60$). Observed rates of change on six islands studied from 8 to 31 years based on census data show an average decline of 2.3% per annum, weighted by number of years (our unpubl. res.). Additionally, of 15 BBS routes within 100-km of the center of our study area and more than 10 years of data, 12 had negative trend estimates, four reaching statistical significance (Table 3.4; Sauer et al. 2005).
Discussion

Patterns in population growth rate

Despite empirical evidence for source-sink dynamics from a broad suite of species (see Harrison & Taylor 1997) and work implicating the role of predators and parasites in shaping these dynamics (Namba et al. 1999; Barabás et al. 2004), we understand little about how landscape structure affects demography and regional population persistence in the presence of an enemy. This study is unique in its incorporation of the distribution and impact of a key enemy on the regional persistence of a host species using empirical data. We examine the distributions of both parasite and host as well as how these distributions affect host reproductive success. Our results suggest that there is spatial variation in the population growth rate ($\lambda$) of sparrows across the study area, which is driven by cowbird parasitism. Further, variation in parasitism appears to influence whether a population is a source ($\lambda > 1$) or a sink ($\lambda < 1$).

Since spatial variation in parasitism rates is driven by the location of cowbird feeding areas, namely urban areas and farms with cattle, these also influence song sparrow population performance. Indeed, sparrow populations further from feeding areas have a higher predicted reproductive success, confirming our hypothesis. Low values of $\lambda$ predicted in a band through the center of the study area are a result of their proximity to livestock and urban areas (Fig. 3.4). Predicted population sources were concentrated on large islands (Saltspring, Galiano) in the north of the study area, isolated from landscape features associated with cowbirds (Fig. 3.4). Rapid declines in parasitism with increasing distance to cowbird feeding areas in urban (Chace et al. 2003) and livestock pastures (Goguen & Mathews 2000) are also known from the western US. Together, these results
suggest that management in support of vulnerable hosts could encourage land use configurations that limit the distribution of cowbird feeding areas to maintain host refuges from parasitism.

Our model predicts a stable regional song sparrow population in the Southern Gulf Islands, but a decline of 8% per annum in the southwest portion of the study area where our demographic studies took place. Within this area, the Mandarte population has declined since 1960 amid high variability overall, and five other study islands have also declined over the past 18 years, with an average decline overall of 2.3% per annum (our unpubl. res.). In the greater region, 12 of 15 BBS routes within 100-km of the center of our study area and more than 10 years of data had negative trend estimates, four reaching statistical significance (Table 3.5; Sauer et al. 2005). Because our predictions fall within the bounds of trends estimated from census data of island populations and from BBS surveys, these independent datasets validate our results.

MODELLING APPROACH

All modelling approaches depend on the suite of assumptions on which they are based, and our results were clearly sensitive to estimates of adult and juvenile survival (Fig. 3.5). Our empirical estimate of juvenile survival (S_j) for our subset of 10 islands was extremely low (mean = 0.05), likely complicated by juvenile dispersal and the small size of some of these populations (Wilson & Arcese In prep.). Juvenile survival rates are particularly difficult or even impossible to determine empirically, but they are critical to the understanding of population dynamics (Anders & Marshall 2005). Their estimation may be further complicated by density-dependent effects, as suggested by decreases in juvenile survival with increasing population density on Mandarte Is. (Smith et al. 2006b).
Thus, we followed previous studies and estimated $S_j$ as 50% of $S_f$ (Greenberg 1980; Temple & Cary 1988; Lloyd et al. 2005), and evaluated the sensitivity of our model to this estimate. This estimate of $S_j$ was within the range of estimates documented on our study site and in other regions (Table 3.5). Adult survival is similarly variable (i.e. see Arcese et al. 2002), but we have more confidence in our empirical rates. Survival of both adults and juveniles seems to be higher on Mandarte Is. than many other locations, perhaps because its isolation discourages predators as well as juvenile dispersal. Clearly, accurate estimates of population status and trend depend on long-term, in-depth demographic studies that can provide reliable empirical estimates (Stacey & Taper 1992; Anders & Marshall 2005). However, validating results of predictive studies with independent estimates of population trend from local and regional sources helps to establish the range within which predicted values should fall.

By predicting an overall stable regional population of song sparrows compared to slight declines in local and regional estimates, our predictions of $\lambda$ may offer a slightly optimistic estimate of growth rates in the Southern Gulf Islands. This optimism may result because survival is higher in the island populations we studied than in the urban and rural areas where BBS trends indicate declines, because parasitism occurs at lower rates in our study area than in habitats experiencing declines, or because changes unrelated to parasitism are reducing population numbers where BBS routes occur. Zanette et al. (2005) also reported that female nestling survival was reduced in parasitized song sparrows nests, whereas we assumed a 1:1 sex ratio, potentially overestimating the annual number of breeding females where parasitism occurs. In addition, any boundary
imposed on a study area may create a biased sample, because trends are a product of local demography, but also of dispersers from outside the focal area.

Many factors affect the reproductive output of any species, such as population density, climate, habitat features, predation, and competition. Several studies have evaluated the effects of predation and cowbird parasitism on songbird population dynamics using the approach of Pease and Grzybowski (1995). For example, Woodworth (1999) found that parasitism by shiny cowbirds *Molothrus bonariensis*, rather than predation by introduced mammalian predators, is likely the cause of declines of the Puerto Rican vireo *Vireo latimeri*. Clearly, the relative importance of parasites and predators as enemies affecting population dynamics will depend on the intensities of each and the life history of the host in question (Grzybowski & Pease 2000). While predation also influences song sparrow populations in our study area, it was not the focus of this study. We tested whether variation in parasitism by a nonnative parasite was sufficient to drive source-sink dynamics in a regional host population. Our approach is based on strong evidence that populations experiencing high rates of parasitism are reproductive sinks (Smith et al. 1996; Rogers et al. 1997) and that parasitism is the probable mechanism (Smith et al. 2002). However, because parasitism and depredation rates of song sparrows are strongly correlated among years and different populations (Arcese & Smith 1999), it is possible that spatial variation in predation would be similar to parasitism, thus reinforcing our predictions.

**IMPLICATIONS OF SOURCE-SINK DYNAMICS**

Spatial variation in reproductive output has the potential to create source-sink dynamics, influence immigration rates, and potentially influence the genetics of
populations (reviewed in Kawecki 2004). Here, we have presented our landscape and populations as static sources and sinks, but these regional population structures persist only with dispersal. Our study system is an archipelago of spatially discrete islands, with smaller, isolated islands existing as populations and larger or less isolated islands comprising patches of varying quality and extent. Natal dispersal between island populations occurs regularly, though less often as isolation increases (Smith et al. 1996; Wilson & Arcese In prep.). Although smaller islands (Imrie, Strawberry) have shown episodes of colonization and extinction within the duration of the long-term study (Wilson & Arcese 2006; our data), larger and more connected populations probably never go extinct or are rescued by immigration prior to extinction (Brown & Kodric-Brown 1977; i.e. Stacey & Taper 1992). Such rescue, however, is less likely in human-modified landscapes as habitat fragmentation continually increases the distance between populations. In the absence of cowbirds, our models suggest growing populations, more dispersers, higher rates of re-colonization of extinct patches, and higher occupancy rates of marginal habitats.

We attempted to locate potential spatial refuges where hosts may be free of the effect of parasitism. The refuge is an old concept in ecology, particularly as a stabilizing force in predator-prey and parasite-host dynamics (Huffaker 1958), and is frequently a focus of studies pertaining to biological control and epidemiology. Although it is particularly useful for basic and applied ecology (Berryman & Hawkins 2006), the refuge is seldom, and then generally implicitly, considered in conservation biology. Examining source-sink dynamics provides one way to approach the refuge concept, as stable source populations represent refuges. Local-scale studies that ignore source-sink dynamics may
not be able to detect declining population trends because they are masked by continued immigration from source populations, even if regional population viability is at risk (Brawn & Robinson 1996). Critical factors seeming to tip the balance to declining regional populations include higher numbers of sink populations relative to sources (Vuilleumier & Possingham 2006), increasing fragmentation of populations (Donovan et al. 1995a; With & King 2001), dispersal from areas more favorable for reproduction to areas less favorable, and declines in the reproductive strength of source populations (Donovan et al. 1995a). Thus, conservation strategies need to recognize source-sink dynamics and protect important source populations.

Few studies have examined population growth rates considering enemies or threats and land use. Modelling the effects of enemies on population dynamics using habitat fragmentation as a surrogate, Donovan et al. (1995a) found that declines in metapopulations were predicted with increasing fragmentation of source habitats. Lloyd et al. (2005) took this approach further and mapped potential population growth rates for the ovenbird *Seiurus aurocapilla* and the wood thrush *Hylocichla mustelina* in relation to forest cover throughout the eastern U.S. Recent studies have used similar combinations of habitat models and demographic data to our study, parameterizing spatially explicit population models (SPEMs) and evaluating population viability and the effect of future scenarios of land use on sensitive species (Carroll et al. 2003; Carroll et al. 2006). For example, Carroll et al. (2003) found that refuges of core habitat were critical to whether potential reintroduction areas could maintain wolves *Canis lupus* under future land use scenarios. All these studies demonstrate the growing importance of understanding the effects of habitat and human land use change on species conservation. Likewise, our
results show that for species with reliable demographic models, landscape-level studies of host and prey species can be used to identify likely source and sink populations and potential refuges from key enemies.

By directly estimating the consequences of parasitism, our results suggest that further spread in the distribution of a nonnative brood parasite and increases in rates of parasitism experienced by a host species may also cause a regional population to decline. Conversely, management of parasite populations may promote the persistence of host species. This study drew on a wealth of data for a well-known model species, but our results can be generalized to hosts that are not as well understood. Parasitism reduces reproductive success in many hosts besides song sparrows (e.g. Robinson et al. 1995; Ward & Smith 2000; Hoover 2003), although some cowbird hosts do not experience net increased reproductive success with cowbird removal (e.g. Stutchbury 1997). Thus, appropriate land management could be critical to maintaining stable songbird populations. Due to the strong influence of urban areas and cattle on parasitism rates, it is recommended that managers consider limiting the proximity of these land uses to predicted source populations in order to preserve these refuges for host populations.

Conclusions

Our results suggest that brood parasitism by brown-headed cowbirds drives spatial variation in the population performance of a host species, and imply that these patterns are likely very different from those prior to the invasion of cowbirds (circa 1955). Decisions to restrict certain land uses in proximity to identified refuges could contribute to the persistence of host populations, and maps such as those presented in this
paper would support such planning efforts. By synthesizing previous approaches and extending beyond what has been seen in the literature to date, our approach shows potential for future studies looking to explore population dynamics of a species with respect to the effect of a key enemy or create other related 'threat maps.' Such tools can help focus land use strategies and management, by illuminating possible mechanisms and highlighting areas suitable or most critical for land protection, restoration, or reintroduction efforts. Although we have not explicitly included dynamic aspects of populations such as dispersal and stochasticity, a next step in this research is to create a spatially explicit metapopulation model parameterized with the extensive data locally available for song sparrows.
Table 3.1: Descriptions of predictive variables used in analyses of song sparrow and cowbird occurrence, their parent GIS layer, and variable abbreviation.

<table>
<thead>
<tr>
<th>Variable Description</th>
<th>Source</th>
<th>Code</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Landcover</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ecosystem Mapping: landcover digitized from orthophotos into 7 classes: Agriculture (AG), Rural (RW), Herbaceous (HB), Wet Habitats (WE), Mature Forest (MF), Woodland (WD), Young Forest (YF)</td>
<td>Islands Trust Ecosystem Mapping (EM)</td>
<td>EM</td>
</tr>
<tr>
<td>Landsat landcover classified into 8 classes: Exposed Land, Herb, Shrub, Wetland, Broadleaf, Sparse Coniferous, Open Coniferous, Dense Coniferous</td>
<td>Landsat TM</td>
<td>LSAT</td>
</tr>
<tr>
<td>Landcover collapsed into forest (≥10% crown closure) vs. nonforest</td>
<td>Landsat-derived</td>
<td>FOR</td>
</tr>
<tr>
<td>Landcover collapsed into 4 levels of crown closure (1=0-10% closure; 2=10-25%; 3=26-60%; 4=60-100%)</td>
<td>Landsat-derived</td>
<td>CCS</td>
</tr>
<tr>
<td><strong>Landscape Variables</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>For Song Sparrows</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance to closest shrub cover (m)</td>
<td>Landsat-derived</td>
<td>DSH</td>
</tr>
<tr>
<td>Proportion of shrub within a 100 m radius</td>
<td>Landsat-derived</td>
<td>PSH1</td>
</tr>
<tr>
<td>Proportion of shrub within a 200 m radius</td>
<td>Landsat-derived</td>
<td>PSH2</td>
</tr>
<tr>
<td>Distance to fresh water (streams, lakes, wetlands) (m)</td>
<td>TRIM</td>
<td>DWAT</td>
</tr>
<tr>
<td>Distance to ocean (m)</td>
<td>EM-derived</td>
<td>DOC</td>
</tr>
<tr>
<td>Variety of land cover classes within a 100 m radius</td>
<td>Landsat-derived</td>
<td>HET1</td>
</tr>
<tr>
<td>Variety of land cover classes within a 200 m radius</td>
<td>Landsat-derived</td>
<td>HET2</td>
</tr>
<tr>
<td>Proportion of forest within a 2.5 km radius neighborhood</td>
<td>Landsat-derived</td>
<td>PFOR</td>
</tr>
<tr>
<td><strong>For Brown-Headed Cowbirds</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance to urban, represented by a town on Vancouver Island (Sidney) harboring the largest population centre close to islands (m)</td>
<td>Aerial photos</td>
<td>DURB</td>
</tr>
<tr>
<td>Distance to nearest agriculture (m)</td>
<td>EM-derived; aerial photos</td>
<td>DAG</td>
</tr>
<tr>
<td>Proportion of farms with cattle within a 2.5 km radius circle neighborhood</td>
<td>Local expertise, Field data</td>
<td>PCAT</td>
</tr>
</tbody>
</table>
Table 3.2: Data used to estimate the relationship between observed probability of occurrence and average parasitism rate experienced by song sparrows. Average parasitism is derived from 1-8 years of data from 15 sites, controlling statistically for number of nests and inter-annual variation via season length.

<table>
<thead>
<tr>
<th>Site</th>
<th>No. n</th>
<th>Years</th>
<th>Parasitism(^1)</th>
<th>Mean Cowbird Occur. ((n))(^3)</th>
<th>Site Size</th>
<th>Island/ Mainland</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Average Rate</td>
<td>Upper 95% CI</td>
<td>Lower 95% CI</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Darcy</td>
<td>2</td>
<td>1998-1999</td>
<td>0.113</td>
<td>0.829</td>
<td>0.198</td>
<td>0.273 (11)</td>
</tr>
<tr>
<td>Dock 1</td>
<td>8</td>
<td>1998-2005</td>
<td>0.459</td>
<td>0.617</td>
<td>0.304</td>
<td>0.538 (13)</td>
</tr>
<tr>
<td>Dock 2</td>
<td>8</td>
<td>1998-2005</td>
<td>0.407</td>
<td>0.568</td>
<td>0.255</td>
<td>0.846 (13)</td>
</tr>
<tr>
<td>Dock 3</td>
<td>6</td>
<td>1998-2001, 2003,2005</td>
<td>0.120</td>
<td>0.300</td>
<td>0.016</td>
<td>0.000 (6)</td>
</tr>
<tr>
<td>Imrie</td>
<td>5</td>
<td>2001-2005</td>
<td>&lt;0.001</td>
<td>0.054</td>
<td>0.062</td>
<td>0.167 (12)</td>
</tr>
<tr>
<td>Ker</td>
<td>8</td>
<td>1998-2005</td>
<td>0.467</td>
<td>0.613</td>
<td>0.324</td>
<td>0.409 (22)</td>
</tr>
<tr>
<td>Little Shell</td>
<td>7</td>
<td>1999-2005</td>
<td>0.434</td>
<td>0.602</td>
<td>0.273</td>
<td>0.308 (13)</td>
</tr>
<tr>
<td>Mandarte</td>
<td>8</td>
<td>1998-2005</td>
<td>0.006</td>
<td>0.037</td>
<td>0.001</td>
<td>0.000 (8)</td>
</tr>
<tr>
<td>Reay</td>
<td>8</td>
<td>1998-2005</td>
<td>0.119</td>
<td>0.251</td>
<td>0.032</td>
<td>0.250 (12)</td>
</tr>
<tr>
<td>Sidney</td>
<td>4</td>
<td>1998-1999, 2001,2003</td>
<td>0.030</td>
<td>0.189</td>
<td>0.011</td>
<td>0.111 (27)</td>
</tr>
<tr>
<td>Piers</td>
<td>2</td>
<td>2005-2006</td>
<td>0.338</td>
<td>0.999</td>
<td>0.099</td>
<td>0.560 (25)</td>
</tr>
<tr>
<td>Rum</td>
<td>1</td>
<td>2006</td>
<td>0.019</td>
<td>-</td>
<td>-</td>
<td>0.063 (16)</td>
</tr>
<tr>
<td>Westham</td>
<td>3</td>
<td>1995,1998-1999</td>
<td>0.689</td>
<td>0.877</td>
<td>0.462</td>
<td>0.850 (20)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deas</td>
<td>2</td>
<td>1997-1998</td>
<td>0.785</td>
<td>0.968</td>
<td>0.172</td>
<td>0.700 (20)</td>
</tr>
<tr>
<td>Delta</td>
<td>3</td>
<td>1996-1997, 1999</td>
<td>0.546</td>
<td>0.783</td>
<td>0.297</td>
<td>0.400 (20)</td>
</tr>
</tbody>
</table>

\(^1\) Reported in original (back-transformed) units with asymmetrical confidence limits (per Sokal & Rolph 1985).

\(^2\) Number of nests reported is pooled for all years.

\(^3\) Mean cowbird occurrence was estimated over multiple site visits, with sample size given in parentheses.
Table 3.3: Subset of sites from Table 3.2 used to estimate reproductive output for song sparrows in a general linear mixed model as determined by data availability.

<table>
<thead>
<tr>
<th>Site</th>
<th>n</th>
<th>Years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dock 1</td>
<td>8</td>
<td>1998-2005</td>
</tr>
<tr>
<td>Dock 2</td>
<td>7</td>
<td>1998-2004</td>
</tr>
<tr>
<td>Imrie</td>
<td>5</td>
<td>2001-2004</td>
</tr>
<tr>
<td>Ker</td>
<td>7</td>
<td>1998-2004</td>
</tr>
<tr>
<td>Little Shell</td>
<td>6</td>
<td>1999-2004</td>
</tr>
<tr>
<td>Mandarte</td>
<td>8</td>
<td>1998-2005</td>
</tr>
<tr>
<td>Reay</td>
<td>8</td>
<td>1998-2004</td>
</tr>
<tr>
<td>Rubly</td>
<td>6</td>
<td>1998-2003</td>
</tr>
<tr>
<td>Strawberry</td>
<td>2</td>
<td>2001-2002</td>
</tr>
</tbody>
</table>
Table 3.4. Song sparrow population trend estimates derived from BBS routes (with ≥10 years of data) within 100 km of study area. Direction and size of trend is given in β, significant trends (P ≤ 0.10) are denoted with *. Data are analyzed using a linear route-regression approach based on estimating equations, and data and analyses are provided in Sauer et al. (2005).

<table>
<thead>
<tr>
<th>Route</th>
<th>β</th>
<th>P</th>
<th>n (years)</th>
<th>Ave. count</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>British Columbia</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Albion</td>
<td>-1.00</td>
<td>0.298</td>
<td>32</td>
<td>34.38</td>
</tr>
<tr>
<td>Chemainus</td>
<td>-4.75</td>
<td>0.104</td>
<td>17</td>
<td>27.94</td>
</tr>
<tr>
<td>Coquitlam</td>
<td>-5.95</td>
<td>0.014*</td>
<td>10</td>
<td>34.40</td>
</tr>
<tr>
<td>Nanaimo River</td>
<td>0.38</td>
<td>0.702</td>
<td>25</td>
<td>18.44</td>
</tr>
<tr>
<td>Point Grey</td>
<td>-4.45</td>
<td>0.001*</td>
<td>12</td>
<td>11.83</td>
</tr>
<tr>
<td>Port Renfrew</td>
<td>-0.41</td>
<td>0.672</td>
<td>21</td>
<td>19.81</td>
</tr>
<tr>
<td>Squamish</td>
<td>1.36</td>
<td>0.841</td>
<td>15</td>
<td>12.53</td>
</tr>
<tr>
<td>Sunshine Coast</td>
<td>-5.16</td>
<td>0.086*</td>
<td>12</td>
<td>7.25</td>
</tr>
<tr>
<td>Victoria</td>
<td>-6.26</td>
<td>0.044*</td>
<td>23</td>
<td>11.57</td>
</tr>
<tr>
<td><strong>Washington State</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bayview</td>
<td>-0.07</td>
<td>0.967</td>
<td>13</td>
<td>22.85</td>
</tr>
<tr>
<td>Hurricane Ridge</td>
<td>-5.89</td>
<td>0.428</td>
<td>11</td>
<td>5.82</td>
</tr>
<tr>
<td>Kendall</td>
<td>-2.44</td>
<td>0.101</td>
<td>24</td>
<td>20.79</td>
</tr>
<tr>
<td>Ozette</td>
<td>-0.93</td>
<td>0.351</td>
<td>33</td>
<td>32.39</td>
</tr>
<tr>
<td>Port Angeles</td>
<td>-2.18</td>
<td>0.160</td>
<td>34</td>
<td>37.15</td>
</tr>
<tr>
<td>Warm Beach</td>
<td>0.83</td>
<td>0.402</td>
<td>37</td>
<td>33.0</td>
</tr>
</tbody>
</table>
Table 3.5: The estimates of apparent juvenile survival below, from populations within our study area and other studies, show the range of variation possible. Estimates from our data are females only, whereas those reported from other species are pooled sexes and likely overestimating female juvenile survival.

<table>
<thead>
<tr>
<th>Location</th>
<th>Mean</th>
<th>SD</th>
<th>Min</th>
<th>Max</th>
<th>Median</th>
<th>No. Years</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mandarte</td>
<td>0.332</td>
<td>0.189</td>
<td>0.019</td>
<td>0.764</td>
<td>0.309</td>
<td>31</td>
<td>Our data</td>
</tr>
<tr>
<td>Dock 1</td>
<td>0.017</td>
<td>0.044</td>
<td>0.000</td>
<td>0.118</td>
<td>0.000</td>
<td>7</td>
<td>Our data</td>
</tr>
<tr>
<td>Dock 2</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>7</td>
<td>Our data</td>
</tr>
<tr>
<td>Dock 3</td>
<td>0.017</td>
<td>0.037</td>
<td>0.000</td>
<td>0.083</td>
<td>0.000</td>
<td>5</td>
<td>Our data</td>
</tr>
<tr>
<td>Imrie</td>
<td>0.038</td>
<td>0.048</td>
<td>0.000</td>
<td>0.100</td>
<td>0.025</td>
<td>4</td>
<td>Our data</td>
</tr>
<tr>
<td>Ker</td>
<td>0.052</td>
<td>0.090</td>
<td>0.000</td>
<td>0.200</td>
<td>0.000</td>
<td>7</td>
<td>Our data</td>
</tr>
<tr>
<td>Little Shell</td>
<td>0.006</td>
<td>0.016</td>
<td>0.000</td>
<td>0.038</td>
<td>0.000</td>
<td>6</td>
<td>Our data</td>
</tr>
<tr>
<td>Reay</td>
<td>0.036</td>
<td>0.061</td>
<td>0.000</td>
<td>0.125</td>
<td>0.000</td>
<td>7</td>
<td>Our data</td>
</tr>
<tr>
<td>Rubly</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>7</td>
<td>Our data</td>
</tr>
<tr>
<td>Strawberry</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>2</td>
<td>Our data</td>
</tr>
<tr>
<td>Point Reyes, CA¹</td>
<td>0.20</td>
<td>0.07</td>
<td>0.16</td>
<td>0.32</td>
<td>0.20</td>
<td>4</td>
<td>Halliburton &amp; Mewaldt 1976</td>
</tr>
<tr>
<td>Ohio¹</td>
<td>0.104</td>
<td>0.051</td>
<td>0.045</td>
<td>0.200</td>
<td>0.091</td>
<td>7</td>
<td>Nice 1937</td>
</tr>
<tr>
<td>San Francisco Bay</td>
<td>~0.20</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>6</td>
<td>Johnston 1956.</td>
</tr>
</tbody>
</table>

¹ Higher estimates for these populations found in Arcese et al. (2002) are calculations including expected dispersal rates rather than apparent survival.
Figure 3.1: The Southern Gulf Islands are on the border between British Columbia, Canada (shaded) and Washington State, U.S.A. (striped). The demographic data come from the area delineated by the dashed line.
Figure 3.2: Relationship between the observed probability of occurrence (presence) of brown-headed cowbirds and average parasitism rates experienced by song sparrows in 15 different sites in (a) transformed and (b) original units.
Figure 3.3: Map of expected cowbird parasitism rates of song sparrows.
Figure 3.4: Map of expected population growth rates for song sparrows considering the impact of parasitism. 'No Song Sparrows' indicates where song sparrows were not predicted to occur based on a 0.70 threshold for probability of occurrence. No strong sources ($\lambda > 1.10$) were predicted.
**Figure 3.5:** Sensitivity analysis for expected population growth rate with variation in adult and juvenile survival rates (a-b), shown as our estimates (solid lines) ± 1 SD (dashed lines; $S_f = 0.500 \pm 0.316$; $S_j = 0.250 \pm 0.158$), and for the strength of the relationship between parasitism and reproductive output (c), using the base parameter estimate ± 1 SE (solid and dashed lines, respectively; $\beta = 0.308 \pm 0.130$).
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Chapter 4: Conclusions

Thesis Summary

Landscape features can influence the spatial structure of populations and have consequences for local dynamics. In particular, spatial variation in the distribution of enemies and their effects on competitors, prey, or hosts can maintain stability in systems (Tilman & Kareiva 1997), but these systems can also become destabilized by human land conversion when this results in the removal of refuges from predation, parasitism or competition. In the absence of refuges, species first impacted by generalist enemies may suffer demographically or become extirpated, whereas the enemies themselves often persist by switching to other prey or host species (Grzybowski & Pease 1999). Thus, to predict if a particular species is likely persist at the regional scale, it will often be necessary to understand how spatial variation in population structure, demographic rates, and the effects of key enemies are distributed in relation to landscape features. This thesis focuses on those elements of populations using a model host-parasite system, the brown-headed cowbird *Molothrus ater* and the song sparrow *Melospiza melodia*.

Habitat Models and Predicting Cowbird Distribution

Habitat models are widely employed to understand wildlife-landscape associations, but many authors have urged a fuller application of available methods. Using presence/absence data from stratified random point count observations, I improved standard logistic regression models for cowbirds by incorporating spatial autocorrelation. In the past few years interest in autologistic models has grown, and they seem to perform better than standard models on all accounts (Klute et al. 2002; Lichstein et al. 2002; Betts
et al. 2006; Priorecky & Prescott 2006; Wintle & Bardos 2006). These models show great promise for conservation biologists as a statistically appropriate way to incorporate landscape and other spatial patterns into the predictive framework. The predictive power of my models was strong (AUC ~ 0.74 – 0.78), but lower than some exceptional rates in the literature (i.e. 0.98; Gibson et al. 2004). Overall, the autologistic model had the most support and seemed sufficient to predict cowbird distribution on the landscape. All cowbird models were robust to internal validations using bootstrapping and when compared to an independent empirical dataset of parasitism rates of a focal host species, the song sparrow, on 12 island study sites monitored for up to 8 years. Although Chace et al. (2005) questioned the validity of correlating the abundance of cowbirds with parasitism frequency, Donovan et al. (1995b) showed that they were related. My results demonstrate that probability of cowbird occurrence was closely and positively related to probability of parasitism in a highly preferred host species.

A cowbird habitat model created with only widely available datasets performed only slightly poorer than full models. This indicates that in some cases land managers will be able to use widely available data rather than investing in expensive data with a more limited geographic scope or intensive surveys. However, in the case of cowbirds, these models convey different information biologically, especially with respect to the inclusion of feeding area variables, which are shown to have strong influences on cowbird distribution at the landscape scale (Chace et al. 2005). In addition, this result also conveys some uncertainty in the selection of ‘best’ models, although our autologistic model was better by recognized standards (ΔAIC>2; Burnham & Anderson 2002). For local cowbird management, I recommend the use of the autologistic model of cowbird
occurrence; however, if managers wished to use a broader extent than what is available for the autologistic model, they could either use the simple model or collect more data. Given that the use of these different models for management may have very different consequences, future studies that evaluate these consequences under different scenarios would be useful.

My comparison of spatial models representing different a priori hypothesis about which factors have the greatest impact on cowbird distribution suggested that the best model integrated landscape features including proximity to feeding areas (including urban, suburban, agriculture, and cattle) and landcover. Although no other studies have evaluated different spatial models on cowbird distribution, two studies evaluated models with respect to parasitism rates of hosts. Gustafson et al. (2002) found that landscape models representing the abundance of forest ('forest-dependent') and the configuration of forest areas ('forest-fragmentation-dependent') fit best with parasitism rates of all hosts combined. In replicated rural landscapes, Tewksbury et al. (2006) found that parasitism of yellow warblers *Dendroica petechia* was best predicted by human settlement, represented by an exponential function. It is evident that there remains considerable variation in the predictors of cowbird occurrence and parasitism rates across different landscapes and regions, suggesting that cowbird management strategies need local information about cowbird distribution. Yet all these studies suggest that human land development facilitates cowbird distribution and parasitism of hosts.
REFUGES AND DEMOGRAPHIC EFFECTS OF COWBIRDS

I show that cowbird parasitism is a strong predictor of the reproductive output of song sparrows and drives spatial variation in their population growth rates. Proximity to landscape features identified as probable cowbird feeding areas determined whether a population was a source or a sink. Although the overall predicted trend in my study landscape was about stable, some indications suggest that my predictions are optimistic. In particular, independent estimates of local and regional population trend based on long-term censuses suggest that song sparrows are declining regionally at rates of c. 1-8%. However, song sparrow populations documented to be strong sinks still maintained constant local abundances (Rogers et al. 1997; Smith et al. 2002), implying sufficient demographic rescue from nearby sites. My results also suggest that growth rates of sparrows are lower than prior to cowbird invasion. Although certain important parameters like dispersal are absent, the weight of evidence would suggest that parasitism by cowbirds does destabilize the system and may threaten song sparrow persistence. However, as song sparrows are relatively tolerant of cowbird parasitism (Smith et al. 2006a), a bigger risk may result if similar demographic patterns exist for more vulnerable host species.

Others interested in generalizing my results on the regional effect of cowbirds on song sparrows should be able to do so given that several points are considered. First, song sparrows in coastal BC can be highly productive, completing up to six nests and four successful broods annually (Smith et al. 2006b). First nests are often completed before cowbirds begin to breed, particularly in warm years when sparrows may breed up to 6 weeks earlier than cowbirds (Smith & Arcese 1994; Smith et al. 2006a). Second,
song sparrows are also more successful than many small-bodied hosts at raising their own young in parasitized nests (Lorenzana & Sealy 1999), and thus tolerate the effects of parasitism reasonably well (Smith et al. 2002; Smith et al. 2006a). As a consequence, my results may underestimate the overall effect of cowbirds on more vulnerable hosts, particularly those with short laying seasons. Third, song sparrows tend to breed in early-successional habitats, but cowbird preferences for breeding areas may differ depending on the suite of available hosts in relation to available habitats. Only a few other studies have tried to actually quantify the effect of cowbirds on the population growth rate of hosts, including warbling vireos *Vireo gilvus* (Ward & Smith 2000) and song sparrows (Smith et al. 2002). But in all such studies to date, the potential impacts are large. Several other studies have examined the effect of habitat fragmentation, a close correlate of nest predation and cowbird parasitism, on forest-breeding birds (Temple & Cary 1988; Donovan et al. 1995a; With & King 2001; Lloyd et al. 2005).

One of the goals of this thesis was to locate potential refuges, where hosts may be free of the effect of parasitism, by identifying source populations. Berryman and Hawkins (2006) present the refuge as an integrating concept in ecology and evolution, being especially important to but seldom applied in population ecology. The idea of the refuge is also tied to spatial patterns of risk, as, for example, Kristan & Boarman (2003) examined predation by human-commensal common ravens *Corvus corax* on desert tortoises *Gopherus agassizii*. Other studies considering the impact of enemies on population dynamics have used spatial variation in enemies to drive differences in mortality risk rather than fecundity (Ylonen et al. 2003; Carroll et al. 2006). These differences in approach stem from the different mechanisms by which enemies and
threats have their effect on the species in question. For example, Donovan et al. (1995b) suggested that different mechanisms resulted in three songbird species experiencing different effects of fragmentation. Only one other study of which we are aware which has mapped potential population growth rates thus spatially identifying potential refuges; Lloyd et al (2005) mapped growth rates for the ovenbird Seiurus aurocapilla and the wood thrush Hylocichla mustelina in relation to forest cover throughout the eastern U.S. My study integrates several elements of the approaches above and suggests that where reliable demographic data exist, landscape-level studies of declining species and their key enemies can be used to identify likely source and sink populations and identify potential refuges.

Caveats

All modelling studies depend on the assumptions on which they are based. I made a number of assumptions, including but not limited to: setting juvenile survival relative to adult survival rather than using empirical estimates; only including habitat effects on sparrows via predictions of parasitism, although many factors could be driving habitat-specific fecundity rates; assuming equal density of sparrows across the landscape, although it certainly varies; and not including demographic or environmental stochasticity. However, these assumptions allowed me to simplify a complex system in order to ask questions about species distributions and the effect of an enemy on population dynamics. Validations of my models with empirical estimates of parasitism rates, reproductive output, and population trend suggested that despite these simplifications, I was able to portray this system in an accurate manner.
Implications

Although cowbirds have been extensively studied in the past several decades, findings (i.e. effect on hosts and influence of landscape features) differ among regions, probably because the identity and relative availability of feeding resources differ across regions, making further studies necessary. Ortega et al. (2005) outlined six future research needs, three of which I addressed in part in this thesis: (1) an understanding of host persistence across varying levels of parasitism; (2) potential cowbird responses to habitat restoration and reduction in possible foraging locations; and (3) a better understanding of local and landscape-level factors influencing cowbirds in landscape contexts other than those previously studied. Our predictive distribution maps for cowbirds could be used to make spatial predictions about the impact of cowbirds on particular hosts, as well as to evaluate land use decisions that could potentially influence cowbird abundance and host fitness. Because predictive distributions for other species are also of great use in conservation, in Chapter 2, I evaluated different habitat modelling approaches and made suggestions for future studies, such as the incorporation of spatial autocorrelation, model validation, and thorough evaluation of alternative models and maps.

Mapping the population growth rates of a common host demonstrates that the influence of an enemy on local population dynamics can have regional consequences. Such maps have the potential to direct further research as well as to influence land management decisions relating to conservation priorities. Because cowbirds are an important species to managers but cowbird control is controversial (see Ortega et al. 2005), appropriate land management could be key to maintaining stable songbird
populations. From this and other studies, there seem to be two clear options: (1) preserve larger tracts of forest, reducing the probability that cowbirds will penetrate all the way into the reserve; and (2) manage the configuration of foraging resources available for cowbirds, and limit their distribution and abundance accordingly. In many areas, the first option is likely the most important. However, where forest has already been heavily fragmented, in naturally fragmented systems like our island archipelago, or for non-forest-dependent host species, managing the configuration of feeding areas is the only option. Certain feeding areas (i.e. urban) are more difficult to manage, thus it would be more important to focus on limiting the distribution of livestock feeding opportunities. Future studies could use my models to evaluate how much this is likely to change cowbird occurrence and the distribution of source and sink habitat for song sparrows.

This thesis consolidates spatial information relating the distribution of the brood parasitic cowbird and its host the song sparrow to extensive empirical data on song sparrow population ecology. A next logical step would be to construct spatial models incorporating elements ignored here for the sake of simplicity, such as dispersal, to predict and evaluate the effects of land use change or conservation on the persistence of hosts under parasitism (i.e. Akcakaya et al. 2004; Schumaker et al. 2004; Carroll & Miquelle 2006; Carroll et al. 2006).
References


APPENDIX 1

Evaluation of different spatial neighborhoods (‘clique’; \( n = 477 \)) for autologistic models of brown-headed cowbirds and song sparrows to determine the best neighborhood size. In both cases, the 1200 m neighborhood was chosen, and the autologistic model was iterated until convergence. There were ten and seven iterations for cowbird and song sparrow models, respectively, until parameters converged.

<table>
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<tr>
<th>Model</th>
<th>( \Delta AIC )</th>
<th>( R^2 )</th>
<th>AUC</th>
</tr>
</thead>
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<td><strong>For Cowbirds (K=6)</strong></td>
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<td></td>
<td></td>
</tr>
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<td>Autologistic 200 m</td>
<td>3.57</td>
<td>0.255</td>
<td>0.769</td>
</tr>
<tr>
<td>Autologistic 400 m</td>
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<td>0.255</td>
<td>0.769</td>
</tr>
<tr>
<td>Autologistic 600 m</td>
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<td>0.255</td>
<td>0.769</td>
</tr>
<tr>
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<td>0.770</td>
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<td>0.771</td>
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<td>0.258</td>
<td>0.771</td>
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<tr>
<td>Autologistic 1600 m</td>
<td>3.85</td>
<td>0.255</td>
<td>0.772</td>
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<td><strong>For Song Sparrows (K=7)</strong></td>
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<td></td>
<td></td>
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<td>Autologistic 400 m</td>
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<tr>
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<td>Autologistic 1600 m</td>
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<tr>
<td>Autologistic 1800 m</td>
<td>1.98</td>
<td>0.232</td>
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APPENDIX 2

Univariate comparisons of local and landscape features at point count sites where song sparrows were detected (n = 332) or not (n = 145). All tests employed Mann-Whitney U-statistics, adjusted for multiple comparisons by Bonferroni correction. ¹ Variable descriptions are given in Table 3.1.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Present Mean</th>
<th>SE</th>
<th>Absent Mean</th>
<th>SE</th>
<th>U-test</th>
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<td>&lt;0.001 **</td>
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<td>85.545</td>
<td>19042</td>
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<td>DSH</td>
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<td>0.005</td>
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<td>30115</td>
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¹ Significant at α=0.05 (*) or after Bonferroni correction α*=0.05/10=0.005 (**)
APPENDIX 3

Variable parameters for best logistic and autologistic model for the song sparrow.

Variable descriptions are given in Table 3.1.

<table>
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<tr>
<th>Variable</th>
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<th>SE</th>
<th>P</th>
<th>Exp($\beta$)</th>
<th>Upper 95% CI</th>
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Best logistic model

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<th>Exp($\beta$)</th>
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1 Reference class for EM categorical variable is YF (Young Forest)
APPENDIX 4

Predicted probability of song sparrow occurrence from the autologistic habitat model.