University of Alberta

Sharp-tailed grouse breeding success, survival, and site selection in relation to habitat measured at multiple scales

By

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ABSTRACT

Ground dwelling birds often have low breeding success in landscapes disturbed by cropland or heavily grazed by domestic stock. Predation is the proximate cause of nest failure or death for many birds and areas disturbed by humans often have higher numbers of generalist predators than do more pristine habitats. At smaller scales, changes to vegetation cover or tree encroachment may increase predator efficiency at finding prey. In this thesis, I used habitat measured at multiple extents to explain the breeding success and survival of sharp-tailed grouse (*Tympanuchus phasianellus*), and include scales relevant for predator dynamics at small and large extents. Corvid density was higher and grouse nests were less successful in landscapes (1,600-m extent) with higher proportions of crop and sparsely covered grassland (sparse grassland). Nest success increased with greater heights of concealment cover within 50 m of nests. Chick survival was 0.41 (SE ± 0.08) from hatch to 30 days post-hatch. Hens with more bare grassland and crop within their home range (583 m) were less likely to rear ≥ 1 chick to 30 days. Raptor density was higher in areas with more sparse grassland (non-linear) and wetland (1,600-m extent). Moreover, hen survival was lower in areas with more crop and sparse grassland at broad extents (0.45 ± 0.07 SE vs. 0.62 ± 0.07 SE, 1,600 m). Hence, human-related disturbance was linked with lower reproduction and survival for grouse. My work culminated in a simulation analysis that evaluated how population growth in human disturbed landscapes responded to management alternatives. Those that improved nest success had the largest influence on population growth.

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CHAPTER 1

INTRODUCTION TO THESIS

Breeding success of ground dwelling birds has been associated with human land use at broad spatial extents. Fragmentation from crop, pastureland, and areas heavily grazed by domestic stock have been inversely related to chick production in mid-summer (Baines 1996, Kurki et al. 2000, Calladine et al. 2002). The association between disturbed landscapes and lower breeding success is generally made through interactions with generalist predators. Predators are the proximate cause of death for many ground dwelling birds (Newton 1993), but changes in habitat at small and broad spatial extents likely exacerbate the rate of predation. Human-caused changes at broad scales have been associated with greater predator densities. In Europe, higher densities of fox (*Vulpes vulpes*, Kurki et al. 1998) and corvids (Andrén 1992) were associated with areas having more crop within forest matrices. At smaller extents, the efficiency of predators searching for prey may improve with human-related changes in habitat. For example, areas with lower concealment cover were associated with lower nest success in England (Calladine et al. 2002). Moreover, prairie landscapes naturally devoid of trees may incur greater predation if tree encroachment provides perch sites for avian predators (Paton 1994, Wolff et al. 1999). Hence, understanding the relationship between habitat and breeding success for ground dwelling birds is generally linked to predators. Clarifying the interaction between predators, prey and habitat is an important step in facilitating the appropriate management for the species of interest (Ormerod 2002).

Sharp-tailed grouse (*Tympanuchus phasianellus,* hereafter sharp-tails) are commonly found in grassland habitats in North America. Grasslands have undergone widespread human-related disturbance since European settlement, and sharp-tails have suffered declines in range and number from historic levels during this period (Schroeder and Robb 1993, Giesen 1998, Connelly et al. 1998). I studied the effects of habitat alterations on the dynamics between predator and prey by linking habitat measured at multiple extents with measures of breeding success and survival for sharp-tails. I used extents relevant to the habitat used by grouse and those related to the density and searching efficiency of predators.

The work in this thesis takes the following progressive steps. Chapter 2 examines the habitat measured at 4 extents important for explaining nest success. The broadest extent used was relevant for explaining the density of prominent nest predators (corvids) in this system. Chapter 3 focuses on brood success ($\geq$ 1 chick surviving to 30 days post-hatch/brood) explained by habitat measured at 2 extents. One extent was relevant to the home range for broods, while the other was associated with raptors. In Chapter 4, I used radio-marked chicks to derive survival estimates from hatch to 30 days post-hatch. Early survival is poorly understood (Schroeder and Robb 1993, Lindström 1994, Giesen 1998, Connelly et al. 1998); indeed, this is the first estimate using individually marked chicks that I am aware of for prairie grouse. I also estimated hen survival over the breeding season, and compared these 2 survival estimates (chick, hen) between landscapes categorized as human disturbed vs. continuous at extents relevant to predators. The work culminates in Chapter 5, where I used a life stage simulation analysis (Wisdom et al. 2000) to evaluate management alternatives designed to benefit sharp-tails in more disturbed landscapes. I used a stochastic population model with vital rates derived from individuals in disturbed landscapes, and modified these values based on hypothetical management options. This body of work is presented in 4 self-contained chapters (2-5), which follow a style consistent with the Journal of Wildlife Management.

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CHAPTER 2

RELATING GROUSE NEST SUCCESS AND CORVID DENSITY TO HABITAT: A MULTI-SCALE APPROACH

INTRODUCTION

Breeding success for ground dwelling birds has been associated with fragmentation from crop and pastureland (Klett et al. 1988, Greenwood et al. 1995, Kurki et al. 2000) and areas heavily grazed by domestic stock (Baines 1996, Calladine et al. 2002). The association between human disturbed landscapes and lower breeding success is generally made through interactions with generalist predators (Kurki et al. 2000), which are the proximate cause of death for many ground dwelling birds (Newton 1993).

Human-related change in the composition and structure of habitat affects the density and searching efficiency of predators. At broad scales, change in the composition of habitat has been associated with greater densities of generalist predators. For example, greater densities of fox (*Vulpes vulpes,* Kurki et al. 1998) and corvids (Andrén 1992) were associated with areas disturbed with more crop and pastureland in forest matrices in Europe. At smaller extents, the efficiency of predators searching for prey may improve with changes that reduce concealment from predators, or force prey to group spatially (Gates and Gysel 1978, Smedshaug et al. 2002). Low concealment cover height near nests has been related to greater nest predation for grouse in a variety of systems (Lutz et al. 1994, Baines 1996, Wiebe and Martin 1998). Moreover, the permeability of smaller habitat fragments by generalist predators has been associated with lower nest success for ducks (Pasitschniak-Arts et al. 1998). Further, prairie landscapes naturally devoid of trees may incur greater predation rates if tree encroachment provides perch sites for avian predators (Paton 1994, Wolff et al. 1999). Hence, the relationship between habitat and breeding success for ground dwelling birds can occur at multiple spatial scales. Therefore, clarifying the association between habitat, predators, and prey at multiple extents is an important step in identifying the appropriate scales for directing management for species of interest (Ormerod 2002).

Sharp-tailed grouse (*Tympanuchus phasianellus*, hereafter sharp-tails) are 1 of 4 species of grouse commonly found in grassland habitats in North America. Grasslands have undergone widespread disturbance since European settlement, and concomitant with these changes, prairie grouse have suffered declines in range and number from historic levels (Schroeder and Robb 1993, Giesen 1998, Connelly et al. 1998). I studied the effects of habitat alterations on the dynamics between predator and prey by linking habitat measured at multiple extents with nest success and nest habitat selection for sharp-tails. I used extents relevant to the habitat used by grouse and those related to the density and searching efficiency of common nest predators.

My hypotheses were threefold. First, hens locate nests in areas with optimal concealment cover. Wiebe and Martin (1998) suggested that ptarmigan (*Lagopus leucurus*) avoid nesting in very dense cover because hens are less able to detect and escape mortality from predators. Hence, I predicted that a quadratic relationship (inverted U) would best describe the height of cover used for nests. Second, I predicted that nest success decreases as landscapes become more disturbed with agricultural land (Klett et al. 1988, Greenwood et al. 1995) because of increases in corvid density associated with agriculture (Andrén 1992). Third, I predicted that nest success would increase with greater concealment cover around the nest (Riley et al. 1992), and that nests close to avian perch sites would suffer greater predation (Paton 1994).

I used covariates from ground surveys and GIS data to clarify relationships between response variables (nest use vs. random available nest sites, corvid density, nest success) and habitat, and then with GIS data alone to provide insight on the amount of information lost with this coarser approach.

STUDY AREA

The study occurred across a broad area (1,392 km^2) in the Mixed Grass Prairie of southeastern Alberta (51°45'N and 111°W). The matrix was predominately grassland, with considerable fragmentation by agricultural crops. Topography was primarily flat with moderately rolling hills towards the southeast. Prominent grasses were fescue (*Festuca* spp.) and needle and thread (*Stipa comata*), and common shrubs included western snowberry (*Symphoricarpos occidentalis*), rose (*Rosa* spp.), and willow (*Salix* spp.). Tree cover was patchy with pockets of aspen (*Populus tremuloides*) found in depressions, along north slopes, and around homesteads, but wider encroachment was evident across the matrix. The primary land use was cattle ranching, followed by agricultural crops (wheat, canola, pea). Oil and gas extraction occurred in clusters across the region. Long term precipitation averaged 371 mm per annum in this region (Appendix 2).

METHODS

Sharp-tails are ground dwelling birds that use a lek mating system. Hens nest and rear broods without parental contribution from males. Hens were captured annually in late April from 1999 through 2001 using walk-in funnel traps (Toepfer et al. 1987) at 10-16 leks. Leks were spaced from west to east across the landscape, and provided a range in the proportion of agricultural crop within a 1,600-m extent. Females were fitted with a 14g-necklace radio collar (Holohil Systems, Carp, Ontario, Canada), and located with a portable receiver and 3-element yagi antenna once every 2-3 days during laying. Hens were triangulated from 50-100 m to locate potential nests. When a female was located more than once in the same position, I then triangulated her position daily and if her location was the same, marked it as a nest site after 3 consecutive days. Trimmed native shrubs were pushed into the ground at approximately 15 m and 20 m from the nest to mark the linear direction to the nest in 2 locations at 90° angles. Thereafter, I assessed if nests were still active by taking telemetry readings every 4-5 days from approximately 30 m. Shrub markers were used as a linear guide to where the hen should be sitting if still nesting. To avoid causing abandonment, nests were visited to determine clutch size, number hatched, or depredation if hen was not present at the marked location. A nest was considered successful if $\geq$ 1 egg hatched. I searched for lost hens using a fixed-wing aircraft intermittently over the nesting season.

Habitat Data

Ground Surveyed Data.—Habitat data were recorded immediately after determining nest fate. Nest concealment cover was estimated with a visual obstruction reading pole (Robel et al. 1970) by averaging 3 measurements taken in ordinal directions (north, west, east), read from 2 m away with the pole located at the nest. To estimate cover directly over the nest bowl I placed a 20-cm diameter black disk with 9 25-mm^2 equally spaced white squares in the nest bowl, and counted the number of white squares $\geq$50% blocked by vegetation when viewed from 1 m directly overhead (Roersma 2001). Three 20x50-cm Daubenmire plots were placed 2 m from the nest and estimates of bare ground and residual cover were averaged over the 3 quadrats (Table 2-1). Residual cover included dead organic matter, either standing or lying horizontal litter.

Concealment cover, bare ground, and residual cover were measured again along a 100-m transect centered at the nest and running east to west. Bare ground and residual cover were averaged over 3 measurements (20, 50 and 100 m) along the transect using Daubenmire plots, while concealment cover was averaged from 10 readings with the Robel pole at 10-m intervals, and read from 2 m. Presence of a potential avian perch site within 75 m of a nest was estimated for 2 binary categories: $\leq$75 m and >75 m (Table 2-1). Woody vegetation > 3 m in height was included as a potential perch.

GIS Surveyed Data.—Habitat composition was estimated with Arcview 3.2 (Environmental Systems Research Institute, Inc.) using a Landsat 7 image taken in 1999 at 30 x 30-m resolution. These data were classified using the program PCI Geomatica 8.2 (PCI Geomatics). Aerial photos (1:30,000) and ground truthing were used to improve the accuracy of classification. Accuracy ranged between 80-94.8%

for each class with an overall rating of 85.6% (K_{hat}), based on stratified random ground truthing (Jensen 1996).

Habitat across the study area was categorized into 6 classes: dense grassland (39%), sparse grassland (27%), crop (26%), trees (4%), wetland (2%) and water (2%, Table A-3-1). Dense grassland included areas with perennial grasses and shrub cover. Sparse grassland included areas with perennial grasses and shrub cover, but had more bare ground reflectance than dense grassland. I used ground surveyed data to calibrate the classification for sparse grassland to represent Daubenmire readings with > 25% bare ground. Sparse grasslands were presumably affected by soil type and/or heavy stock grazing over a period of years. Evidence for the relative influence of grazing was anecdotal based on personal communication with landowners and the regional range manager. Crop included cultivated land, hay land cut annually, and anthropogenic disturbance (homesteads, country roads). I included all tree species and willows in 1 category that I defined from ground truthing as woody vegetation > 3 m in height. The density of edge/ha was calculated for habitat classes using the Patch Analyst extension in Arcview 3.2. (Elkie et al. 1999).

Percent habitat composition from the 6 classes summed to 100% and therefore the covariates were not independent when treated as continuous variables (Aebischer et al. 1993). I used log ratios [i.e. $\log(a_i/b)$] to remedy this problem (Aebischer et al. 1993, Kurki et al. 1998) with dense grassland (the most abundant cover class) as the denominator (b) for the remaining 5 classes (a_i). The interpretation was expressed as the influence of habitat a at the expense of habitat b (Kurki et al. 1998). I replaced zero values with 0.001 to make log ratio transformations possible (Aebischer et al.

1993). Log ratio explanatory variables included the relative proportion of crop, sparse grassland, trees, wetland, and water (Table 2-1).

Nest Predators

Common avian nest predators included the American crow (*Corvus brachyrhynchos*) and black billed magpie (*Pica pica*). Mammalian egg predators included coyote (*Canis latrans*), red fox (*Vulpes vulpes*), skunk (*Mephitis mephitis*), ground squirrel (*Citellus spp.*, and Spermophilus spp.) and badger (*Taxidea taxus*). Birds of prey were abundant but not suspected to be prominent egg predators in the region. Corvids were prominent egg predators, identified by beak marks on plasticine eggs, accounting for at least 80% of the predation events from a sample of 77 artificial nests laid out in the area in 1999 (Appendix I). Coyotes were suspected as the prominent mammalian predator.

To estimate how corvid density varied with habitat I conducted surveys twice annually in late May and again in late June or early July in 2000 and 2001. Point counts were made from 0.5 hr before sunrise to 3 hrs after sunrise along 26 3,200-m transects with 5 stations 800 m apart. Transects were randomly located in habitat stratified by the proportion of crop at a 1,600-m extent to ensure surveys were conducted along a gradient of cropland landscapes. Corvids seen or heard at stations and between stations within 400 m of the transect line were recorded and summed over the transect. Habitat was measured using GIS within 1,600 m and 2,265 m circular landscapes centered at the 1,600 m mid-point of the transect. Transects were > 4,530 m apart to avoid double counting the habitat used in the largest buffer (2,265 m x 2).

Spatial Scale

The spatial scales relevant to the nesting ecology of sharp-tails were considered for 3 processes: 1) the habitat selected by grouse for nesting, 2) the extent affecting the density of prominent nest predators, and 3) habitat features at smaller extents that may aid predator efficiency in detecting nests. Hens generally nested within 1,521 m of the nearest lek (95% CI 1,521 m, n = 106 nests), so I used this distance as the extent of habitat available for nest sites around the 16 capture leks. I approximated the extent of habitat used by hens during nesting by measuring the distance between the nest and daily locations with Arcview 3.2 using universal transverse mercator (UTM) readings taken from hand-held GPS units. Locations were generally within 437 m of the nest (95% CI 437 m, n = 27 hens) so I used a radius of 437 m around each nest to measure habitat use during laying and incubation. On a smaller scale (microsite), I considered habitat use within 2 m and 50 m of the nest. The 50-m scale allowed me to use both ground surveyed habitat information and data analyzed with a GIS. These smaller extents (2 and 50 m) were evaluated because I presumed nest selection would occur at these levels and that predators searching for nests could use habitat cues at these scales.

I modeled relative corvid density by habitat composition and edge density measured at 1,600 m and 2,265 m scales to identify the extent most relevant for describing avian predator density. I then used habitat from this extent to model grouse nest success. I assumed extents $\geq$ 1,600 m were adequate to look for patterns between habitat and corvid density because > 1 pair of each species (crow, magpie) are commonly found at these scales. Based on other studies I estimated a density of at least 10 magpie pairs per km^2 (Trost 1999). I searched the literature and found that density estimates for American crows are not well known; however, I estimated that at least 3 pairs probably occur within an 8 km^2 area (1,600 m radius) based on a study in Manitoba (Sullivan and Dinsmore 1992).

Data Analysis

My overall approach was to define *a priori* candidate models based on predictions of how the system worked. Since my knowledge of the system was imperfect, I also built stepwise regression models for comparison with candidate models. Akaike's Information Criteria, corrected for small sample bias (AIC_c), was used to calculate Akaike ranks (ΔAIC_c) and weights (ω_i) for each model. I used ω_i to identify models with the most evidence for fitting the data (Anderson et al. 2000, Anderson and Burnham 2002). The ω_i estimated the probability that model *i* was the best among those considered, and ω_i / ω_j described the approximate likelihood of model *i* being better than model *j* (Anderson et al. 2000: 918). Odds ratios were used to interpret logistic regression results ($e^{\text{beta coeff}}$), and for comparing the ratio of odds between 2 groups of binary data (Ramsey and Schafer 2002: 538). The amount of deviance explained (D, logistic regression: deviance full model/deviance null model) or R^2 (linear regression) were used as descriptive measures of how well the models fit the data (Menard 1995, Ramsey and Schafer 2002). I checked for influential outliers with leverage ratios and studentized residuals (Menard 1995). Where backward stepwise regression was used, alpha values were set at 0.05 for removal and entry of covariates. Regression procedures using categorical explanatory variables required that 1 category be removed, hence I used the category with the highest value as the reference. Year was included as a variable and evaluated for interactions with other covariates in regression procedures. Statistical analyses were performed with Excel, SPSS 11.0 (SPSS Inc.), and Statistica (StatSoft, Inc.) software.

Nest Habitat Selection.—Candidate models were derived as follows. I hypothesized that hens would show selection for taller concealment cover near the nest {vor50; res50; bd50} (Table 2-1), but would avoid very dense cover {vor50+ vor50^2}. Hens may avoid very heavy cover if it hinders their ability to 1) escape predators or 2) detect predators early enough to distract them away from the nest. For GIS data at the 50-m extent, I hypothesized that hens would avoid crop and sparse grassland {crop50+brgr50}. Based on the assumption that avian predators use perch sites to locate nests, I predicted hens would avoid nesting close to treed habitat, or close to wetlands because moist areas often have tall willows {tree50+wet50}. At the 437-m scale, I predicted hens would avoid crop and sparse grassland because these habitats provide poor cover for nesting. However, I assumed hens would select areas with treed habitat at the 437-m extent because another study in Alberta showed hens used tree bluffs (presumably for loafing) during the spring breeding period (Moyles 1981) {crop437+brgr437+tree437}.

Nest selection [use (1) vs. availability (0)] was modeled separately for data surveyed with ground methods and GIS techniques using quasi-likelihood logistic regression (Anderson and Burnham 2000, Ramsey and Schafer 2002). I assumed samples may lack spatial independence at some extent, and therefore applied the quasi-likelihood approach to inflate the standard error (SE) for beta coefficients (Anderson et al. 2000, Ramsey and Schafer 2002). For the GIS analysis, available points were located randomly with Arcview 3.2 within 1,521 m of the nearest lek. Since habitat selection is not well known for sharp-tails, I compared a model derived from backward stepwise regression with 1 *a priori* candidate model at each extent for the GIS data. I did not know the extent of area used for nesting prior to the study, so for ground surveys conducted during the study I used estimates of the space available habitat from the literature (Pepper 1972, Ramharter 1976, Giesen and Connelly 1993). Hence, available points for ground surveyed data were randomly located within 1,600 m of the nearest lek. Covariates from the 50-m ground data were inter-correlated (Pearson correlation, $P < 0.05$) in both 2000 and 2001 so I modeled these variables individually and did not apply backward regression. Model comparisons using ΔAIC_c and ω_i were not made between extents nor between data from different years or survey methods because use and availability differed among these subsets (Anderson and Burnham 2002).

Predator Density and Spatial Extent.—I did not use *a priori* candidate models to evaluate specific hypotheses, however, I did include covariates that would allow me to evaluate inferences derived from previous studies. Based on Andrén's (1992) analysis of corvid density, I assumed that crop habitat would be positively associated with crow density, but less important for magpies. Given the relative scarcity of trees on the prairie landscape, I assumed treed areas could be an important nest and roosting resource and thus be associated with higher densities for both species. Edge habitat can provide multiple prey species for generalist predators (Paton 1994), so I included edge density covariates for crop, tree, and dense grassland habitats.

The analyses were performed in 2 steps. In step 1 (within extents) I regressed corvid density (log transformed, each species separately) on habitat covariates using least squares multiple linear regression for each extent. Hence, models were compared within each extent (1,600 m, 2,265 m) for each species separately. In step 2 (between extents), I ranked the best model between the 2 extents for each species separately using ω_i.

Prior to modeling corvid density with habitat variables, I first assessed if density estimates could be averaged for each species separately (crow, magpie) between years. Hence, I initially looked for a year effect using linear regression and modeled corvid density by year and the habitat covariate with the strongest correlation with density (Andrén 1992). Moreover, I evaluated bivariate relationships between all habitat variables using scatter plots and a correlation matrix. If explanatory variables were highly correlated (> 0.40) they were not used together in the same model. No more than 2 explanatory covariates were used in the same model to avoid over-fitting these data given the moderate number of landscapes sampled ($n \leq 26$).

Nest Success and Habitat.—Candidate models were derived as follows. I hypothesized that concealment cover within 2 m of the nest would increase success linearly {vor2}. I used a quadratic expression to evaluate if heavy cover was a factor for nest success in this system {vor2+vor2^2}. I applied the same rationale for candidate models at the 50 to 75-m scale {vor50; vor50+vor50^2}, but included the presence of perch sites within 75 m of a nest in a third model because I hypothesized avian predators could use these perch sites while searching for nests (Paton 1994) {vor50+vor50^2+perch<75}. I followed a similar line of reasoning for candidate models using GIS data at 50 m {tree50+brgr50; crop50} and 437-m extents {crop437 + brgr437+tree437; crop437}. I hypothesized that crop or crop edge might have a negative relationship with nest success at the 1,600-m extent (Greenwood et al. 1995) {crop16L; e.cpL}. I also aggregated crop and sparse grassland at the 1,600-m scale to create 1 variable that described habitat with lower potential for nesting {crbr16L}. I parameterized the best overall candidate models among all extents and habitat survey approaches with a measure of concealment cover near the nest, and the amount of crop at the 1,600-m extent {vor2+crop16L; vor50+crop16L}.

Nest success was analyzed in 4 steps to address specific objectives using quasi-likelihood logistic regression (Anderson and Burnham 2002). First, the best model for describing nest success was determined within subsets for a) each extent (2 m to 1,600 m) and b) for each habitat survey approach (GIS vs. ground survey). Differentiating models by these categories allowed me to clarify relationships between extents and nest success, as well as identify discrepancies between coarse resolution GIS data and ground surveyed information. I compared *a priori* candidate models with those derived from backward stepwise selection for each subset. I included stepwise regression because knowledge of habitat features associated with sharp-tail breeding success is not well known; thus, I did not want to miss strong associations that I did not predict. Covariates estimating habitat composition and edge density at landscape scales (1,600 m) were based on habitat measurements centered at the nearest lek and were categorized into 3 groups (low, medium and high, Table 2-1). Proportions in each of these 3 groups differed among the habitat classes, and were derived from visually inspecting the distributions for each class (i.e. % crop at 1,600 m, low <10 %, medium = 10–30%, high = 45–70%; Table 2-1). Second, I identified the most relevant extent and habitat survey approach among all subsets for describing nest success based on the suite of models developed from step 1 using ω_i. Third, the best overall model was derived using potential covariates from all extents and both habitat survey approaches. I compared candidate models (ω_i) with the model selected from backward stepwise regression. Covariates used in the backward procedure were limited to those from the best model from each extent and habitat survey method derived in step 1 ($n = 7$ covariates). With the intent of formulating a tool for regional management, a fourth modeling step was taken to estimate the best model using GIS data alone from all possible extents. Similar to step 3, I applied backward stepwise regression allowing potential covariates ($n = 5$) from the best models identified in step 1 for each extent that used GIS data.

The sample of hens was captured at 16 leks across the region. Given that most nests were within 1,521 m (7.29 km^2) of a lek, their distribution was somewhat clumped at a regional scale. However, most organisms are clumped at some spatial extent (Wiens 1989), hence we need to balance assumptions of independence with practical data collection limitations. I considered hens captured at the same lek to be individual sample units because 1) all hens attempted to nest, which implied space was not limited and therefore nests were located independent of other hen choices, and 2) hens were not dependent on males for nesting territories and therefore located nests based on individual preference.

I reduced the likelihood of pseudoreplication between nests due to spatial correlation or individual hen behavior by limiting the sample of nests to 1 per hen. If hens nested in more than 1 year or re-nested in the same year, I randomly selected 1 nest for that hen. I also limited the sample by randomly removing 1 or more nests within 874 m (2 x 437 m = 874 m) of the next closest nest. At the 1,600-m extent, habitat data overlapped for more than 1 observation in some cases. Thus, SE and therefore confidence intervals (CI) for the beta coefficients of 1,600-m covariates, may be underestimated even though I used the scaling mechanism that inflates SE via the quasi-likelihood procedure (Anderson et al. 2000, Ramsey and Schafer 2002). To avoid misleading the reader, I treated 1,600-m scale habitat covariates as categorical (Table 2-1) and ensured that each habitat category had nests from at least 4 different leks to represent patterns in a number of these 8-km^2 landscapes.

RESULTS

Nesting

I monitored 28 radio-collared hens in 1999, 42 in 2000, and 52 in 2001. Apparent nest success was 0.47 ± 0.02 ($\bar{\chi}$ ± SE) based on 107 nest events from individual hens across the study area over 3 years. However, nest success differed markedly between those in areas with <35% vs. ≥35% crop and sparse grassland at the 1,600-m extent (0.68 ± 0.05, n = 41 vs. 0.35 ± 0.05, n = 66, respectively). Re-nesting was common (69%) if the first nest was depredated. Three hens produced 3 nests (2 re-nests) in the same season. Seasonal rainfall was greater than average in 1999, and lower than average in 2000 and 2001 (Appendix 2 Fig A-2-1.).

Nest Habitat Selection

I used 25 nests in 2000 and 33 nests in 2001 to model nest habitat selection with ground data at the 50-m extent. These nests were randomly selected from all potential nests by randomly eliminating 1 or more nests that overlapped at the home range extent (2 x 437 m). Nests from 1999 were not included in this analysis because random ground surveyed data were not collected at the landscape extent in that year. Years were modeled separately because available habitat data corresponded with use data from a single year. Available habitat was measured at 240 and 218 random sites in 2000 and 2001 respectively.

For ground surveyed data, nest selection was best described by the height of concealment cover (vor50) within 50 m of the nest in both years (Table 2-2). In 2001, a quadratic relationship for vor50 was better than using the linear term alone, while in 2000 the linear term was the better model (models 6 and 1 respectively, Table 2-2). Cover height at nests averaged 19.9 cm ± 1.77 and 10.5 cm ± 0.94 in 2000 and 2001 respectively, and at random sites was 4.58 cm ± 0.29 and 4.35 cm ± 0.30 respectively. Concealment cover explained 51 and 21 % of the deviation in habitat selection for nests in 2000 and 2001. The percent cover of bare ground over a 50-m extent was negatively related to used sites in both years, while residual cover was positively related (models 3, 4, 7, 8; Table 2-2).

I used 67 nests from 1999-2001 and 2,786 random locations to model nest selection with GIS data at the 50-m extent. Again, these nests were randomly selected from all potential nests by randomly eliminating 1 or more nests that overlapped at the home range extent (2 x 437 m). Nest site selection at the 50-m extent was best described by a positive association with trees and a negative relationship with wetland (model 9B, Table 2-2).

I used 67 nests and 96 random locations to model nest selection with GIS data at a 437-m extent. The candidate model matched the best model derived from backward selection (Table 2-2, model 11C), but explained only 3% of the deviation. Nest selection was positively related to trees and negatively associated with crop and sparse grassland. The explanatory ability (D) of the best models using GIS habitat data was considerably lower than the best models using ground surveyed methods (Table 2-2).

Corvid Density and Spatial Extent

I averaged density for crows and magpies (separately) over 2 years because YEAR was not significant when used to evaluate the association between corvid density and the strongest habitat variable (linear regression, t values for YEAR effect: crow 1,600 m, n = 26, t = -0.7, P = 0.48; crow 2,265 m, n = 26, t = -0.99, P = 0.33; magpie 1,600 m, n = 25, t = 1.01, P = 0.32; magpie 2,265m, n = 25, t = 0.82, P = 0.42).

Crows.—Crows were counted in all 26 transects in both years. Landscape variables explained up to 32% of the variation (R^2) in log crow density. The model with the largest ω_i from the 1,600-m extent (model 1, Table 2-3) was 1.4 times (ω_i/ω_j) more likely to be better than the best model from the 2,265-m extent. Hence, there was a moderate level of evidence that habitat from the 1,600-m extent was better for describing crow density. The top models from both extents showed that density increased with corresponding increases in sparse grassland on the landscape (data range Fig. A-3-4). The coefficient for sparse grassland was positive for all models from both extents. The edge density of dense grassland was negatively associated with crow density. While crop was not included in the best model, the relationship between crop and crow density was consistently positive where used. Treed habitat was negatively related to density for both extents.

Magpies.—Magpies were counted in 25 of the 26 transects in 2000 and 2001.

Landscape variables were not as effective for explaining relative magpie density as they were for crow density. The best magpie model from either extent (model 19,Table 2-3) explained only 4% of the variation in log magpie density. Further, there was no convincing evidence that the 2,265 m extent was better for describing density compared with the 1,600-m extent (model 13 vs. 19, Table 2-3, ω_i / ω_j, 1.01 times). The top models from each extent included the same covariates, with log magpie density positively associated with increasing amounts of crop and sparse grassland, and the edge density of crop. In contrast to the crow density models, treed habitat was positively associated with magpie density.

The most relevant extent for explaining density with habitat variables was 1,600-m for crows, but not clarified for magpies. Moreover, the variation explained by the best crow model was an order of magnitude greater than that for the best magpie model (models 1 and 19 respectively, Table 2-3). Based on this information, I used the 1,600-m extent to guide my selection of the landscape extent most relevant for inclusion in the nest success analyses.

Nest Success and Habitat

The rationale for linking the extent of habitat features important for explaining corvid density with that for nest success was supported by the strong relationship between corvid density and the outcome of nests in 14 landscapes across the study area. The odds of a hen having a successful nest was 8 times greater in landscapes with < 3 corvids/km^2 compared with areas having ≥ 3 corvids/km^2 (odds ratio, 95% CI 2.54–25.33 times, Fig. 2-2B).

Step One.—The chance of nest success improved as the height of concealment cover increased when measured at 2 and 50-m extents (models 1C and 3C, Table 2-4; data range Table A-3-2). Nests were more likely to succeed for each 1-cm increase in the height of concealment cover at the 50-m scale ($e^{0.19}$, 95% CI 1.07–1.36 times, data range 1.4–34.4 cm). At both extents, a linear function was better than a quadratic term for describing nest success (models 1C vs. 2C, 3C vs. 4C, Table 2-4).

The prediction that crop and sparse grassland would be negatively associated with nest success at broader scales was supported by model 8C at the 437-m extent, and model 10C at the 1,600-m extent (Table 2-4). At both scales, nest success was more likely to occur in landscapes with lower proportions of crop and sparse grassland at the expense of dense grassland. Nests were 5 times (odds ratio, 95% CI 1.6–16.3 times) more likely to succeed in landscapes with <35% crop and sparse grassland compared with those in landscapes with ≥35% (1,600-m extent, Fig. 2-1A).

Step Two.—Concealment cover measured at the 50-m extent (vor50) was the best model using variables from 1 extent to explain nest success (model 3C, Table 2-4).

This model was ≥ 77.1 times (ω_i / ω_j) more likely to be best for describing nest success compared with the other top ranked single scale models (step 2, Table 2-4).

Step Three.— The best overall model using variables from multiple scales described greater success for nests with more concealment cover within a 50-m scale, and in landscapes (1,600 m) with lower amounts of crop at the expense of dense grassland (model 13C, Table 2-4, Fig. 2-1B). Together these 2 covariates explained 30% of the deviation in nest success.

Step Four.— The best model using GIS data from all potential extents (50, 437, and 1,600 m) was derived from broader scale variables (model 16B, Table 2-4; data range, Table A-3-3). Success was positively related to the proportion of trees at the expense of dense grassland (437 m), and more likely to occur in landscapes with lower proportions of crop and sparse grassland (1,600 m). Tree cover averaged 10% ± 0.02 at successful and 4% ± 0.01 at unsuccessful nests at the 437-m extent.

Post hoc analysis.—I predicted that nest success would be lower for nests close to perch sites because of the advantage they would offer to a predator in a prairie landscape. However, perch was not included in any of the top models for describing nest success (Table 2-4). I decided to explore the relationship further because 1) hens showed a selection rather than an avoidance for treed habitat at a 50-m extent (model 9B, Table 2-2), and 2) I wanted to clarify whether the benefit of concealment cover for nest success depended on the presence of perch sites within 75 m of a nest. Indeed the relationship between nest success and the presence of perch sites was complex. Success was not statistically affected by the proximity of a perch site upon initial examination (< or ≥ 75 m, 95% CI 0.73–5.1 times, Fig. 2-2A), but perch was important for explaining nest success when evaluated as an interaction term with concealment cover. The interaction with perch was particularly strong when concealment cover was measured over 50 m rather than within 2 m of nests ($\omega_i > 0.99$, D = 20% vs. $\omega_j < 0.01$, D = 8%, models 1 and 2, Table 2-5). Further, the slope for concealment cover (50 m) was moderately steeper for nests within 75 m of perch sites compared with those further away (model 1, Table 2-5). Therefore, after accounting for the effect of perch (perch<75) on nest success, the height of concealment cover became more important for the success of nests within 75 m of a perch site.

DISCUSSION

Nest Success and Habitat Selection

My study suggests that the ecological processes related to nest success occur at scales smaller (50 m) and considerably larger (1,600 m) than the area used by nesting hens ($\approx$437 m). Although nest success was related to habitat measured across a broad spatial range (2–1,600 m), the variables measured at the 50-m extent had the most explanatory power. This suggests that either small-scale ecological processes that influenced predator efficiency were more prominent in this system, or I was not as successful in measuring relevant broad scale habitat variables important to nest success.

Concealment cover was the most important variable for explaining nest success, but the strength of the relationship varied with spatial scale. Cover at the 50-m extent explained more of the deviation in nest success than cover 2 m from the nest. Other studies on prairie grouse have had mixed results using similar measurements of concealment cover near the nest. For example, Lutz et al. (1994) found higher success associated with taller cover close to grouse nests (4 m) in Texas, whereas cover measured at 4 and 8-m extents was not important for explaining success in the tall grass prairie of Missouri (McKee et al. 1998).

There are at least 2 ecological factors that may explain why cover measured at 50 m as opposed to 2 m from the nest was better for describing nest success. First, predators will take more time and effort to search for nests in larger patches of tall concealment cover (Pasitschniak-Arts et al. 1998). Second, larger patches of tall cover would conceal hens from predators as they moved to and from the nest during laying, or to forage while incubating. Movement is likely an important cue used by avian predators looking for nests. Therefore, nests in smaller patches (i.e. 2 m extent) of tall cover might have a greater probability of being detected by predators who have seen the hen moving to or from the nest. This may partially account for the difficulty with predicting nest success from cover variables measured very close to the nest.

If predators use hen movement to detect nests, then nests located close to avian predator perch sites that have less cover at the 50 m scale should have higher predation rates. This was indeed the case: nests that were within 75 m of a perch were more successful if they had taller concealment cover, and this effect was much stronger for cover measured at 50 m than at 2 m. Indeed, the interaction between perch and concealment was important for explaining nest success, and would rank this model as the best among all single scale models evaluated in step 2 of the nest success analysis (based on ΔAIC_c ranks). Hence, measurements of concealment cover close to the nest (2 m) may not be reliable for predicting success because of hen movements beyond this scale. However, I conducted these analyses after completing my initial model comparison, and therefore do not give the evidence the same consideration (Anderson and Burnham 2002). I present the hen movement hypothesis as a process that can be evaluated in future research.

The best overall model for explaining nest success included concealment cover at the 50-m scale and the proportion of crop measured at 1,600 m. This is consistent with the prediction that small and broad scale processes are important for explaining breeding success, and similar to other studies that have demonstrated an inverse relationship between breeding success and increased landscape disturbance (Pepper 1972, Greenwood et al. 1995, Ryan et al. 1998, Kurki et al. 2000, Calladine et al. 2002). More disturbed landscapes often have higher predator densities (Andrén 1992, Kurki et al. 1998, Kurki et al. 2000). In this study, corvid densities were positively associated with crop and sparse grassland at broad scales, whereas nest success was negatively associated with these variables at the same extents. Moreover, nests were 8 times more likely to succeed in landscapes with lower corvid densities (<3 vs. ≥ 3 corvids/km^2). Unfortunately, I do not have direct evidence linking corvids with the success of real nests, since determining the predator species that depredates a nest is difficult to assess consistently (Larivière 1999). However, the majority of depredated nests in an artifical nest experiment in this area had marks consistent with corvid depredation, suggesting corvids are a prominent egg predator in this system (Appendix I).

My prediction that females selected nest sites in high concealment cover was supported and is consistent with other studies on prairie grouse (cover measured 1 to

15 m radius around nest, Pepper 1972, Ramharter 1976, Roersma 2001, Aldridge and Brigham 2002). The prediction that hens avoid placing nests in very dense cover (i.e. a quadratic relationship with cover) was not supported conclusively, and results differed between years. However, an overabundance of dense cover is unlikely in dry and mixed grassland systems where grazing is practiced (Klett et al. 1988), and periodic drought restricts vegetation growth. Moisture likely played a strong role in determining the amount of deviation explained for models in 2000 vs. 2001. Vegetative growth in 2000 followed a good year of moisture in 1999. In contrast, 2001 followed a relatively weak year of moisture in 2000. Average concealment cover height around nests (50 m extent) in 2001 was near 50% of the height in 2000.

At 50 and 437-m extents, hens chose nest sites in areas of high tree cover, and I commonly observed nests located at the periphery of a large shrub patch that contained tall woody vegetation. Sharp-tails often nest under a shrub (Connelly et al. 1998) and females are often located in tall woody patches when off-nest during laying and brood rearing (Moyles 1981). However, these shrubby areas may be ecological traps (Gates and Gysel 1978). Although nest success was positively associated with amount of treed habitat at 467 m and 1,600 m extents, nests were more vulnerable to predation if they were close to perch sites unless adequate nesting cover was available. Nests located near shrub and tree patches may have not only been detected by avian predators, but also by mammalian predators that frequent edge habitats (e.g. coyotes, Winter et al. 2000).

Corvid Density and Spatial Extent

Introducing agriculture into a natural landscape can change the predator community and provide an advantage for generalist predators (Andrén 1992, Kurki et al. 1997, Sovada et al. 2000). I found greater crow and magpie densities in landscapes with greater proportions of crop and sparse grassland (1,600 m). I did not examine the underlying mechanisms between corvids and these disturbed landscapes, but presumably, food generalists can take advantage of new foraging opportunities directly from farms, or from prey species that use these new resources (Andrén 1992). Given the relative scarcity of treed habitat across the study area (4%), I anticipated that corvid density would be greater in areas that provided more roost and nesting sites. However, the results were mixed in that magpie density rose with treed habitat, while crow density declined. Trost (1999) suggested magpies favor treed cover because they are vulnerable to raptors when in more open habitat due to their relatively slow flight and long tails. Hence, crows may be relatively more prone to using agricultural areas while magpies may avoid spaces that are more open.

Density of both corvid species increased as the proportion of sparse grassland increased. Some areas coded as sparse grassland were close to farmyards that may have provided alternative food resources. Further, cattle often grazed in sparse grassland and magpies are known to feed on the ecotoparasites found on domestic stock (Trost 1999). Moreover, I observed that sparse grassland areas had high numbers of grasshoppers that presumably hatched on the bare soils, and may have been used as a food resource by corvids.

Variation in crow density was much better explained by habitat variables than was magpie density, suggesting that the extents I used to measure habitat better represented ecological processes affecting crows. Caccamise et al. (1997) found that crows commonly forage large distances from their territories during the day (up to 4 km), therefore, broad aerial movement likely increased my ability to detect crows in more open habitats. Alternatively, I may not have measured the habitat features important for magpies, or the resolution of the pixels may have been too coarse. Moreover, magpies generally have smaller territories compared to crows (Caccamise et al. 1997, Sullivan and Dinsmore 1992, Trost 1999), so my extents may have been too large to model a stronger relationship with magpies.

GIS vs. Ground Survey Data

Habitat covariates from GIS data were relatively poor at explaining nest success and habitat selection at small spatial scales, possibly because of the coarse scale of resolution (900 m^2 pixels). Indeed the grain of observation was relatively poor at small spatial extents with GIS data. GIS data was important for evaluating habitat at broader scales, but the best overall model used data from both survey methods. Hence, studies can likely benefit by applying both techniques where *a priori* predictions suggest relevant biological interactions operate at small and broad extents.

Linking Management with Scale

Sharp-tail management should be done at various spatial scales. Efforts to improve nest success by increasing concealment cover for nests or removing perch sites may have limited success if larger scale factors associated with predator densities are not considered. Therefore, a plausible initial step is to identify broad spatial areas with potential for relatively high nesting success. Nests were more likely to succeed in areas with < 10% crop and <35% crop and sparse grassland (aggregated) at the 1600-m extent, hence, landscapes that are close to these thresholds could be prioritized for broad scale management. For example, programs such as Greencover Canada or the Conservation Reserve Program can prioritize marginal cropland for conversion back to perennial grass. If using GIS to quantify habitat, then the aggregated measure of crop and sparse grassland is more applicable than using crop alone to prioritize landscapes for conversion.

Landscapes with potential for high nesting success could then be considered for smaller scale management action. I suggest that the target height for concealment cover be at least 13 cm, and monitored over a 50-m extent rather than smaller scales (i.e. 2 m). The effect of trees (perch sites) was not clear in this study, but tree encroachment may be a problem, and therefore the relationship between trees, concealment cover, and nest success should be pursued in future work.

Table 2-1. Explanatory habitat variables for analyzing grouse nest habitat selection (Sel), corvid density (Cor), and grouse nest success (NS). Categorized by habitat surveyed from ground or GIS methods.

Variable	Data type	Description		Analysis
Ground data				
vor2	continuous	concealment cover height 2m around nest		NS
$vor2^2$	continuous	vor2*vor2 (quadratic term)		NS
overhd	continuous	cover directly over nest		NS
bd2	continuous	bare ground 2m around nest		NS
res2	continuous	residual 2m around nest		NS
vor50	continuous	concealment cover height averaged over a 100m transect centered at nest		Sel, NS
$vor50^2$	continuous	vor50*vor50 (quadratic term)		Sel, NS
bd50	continuous	bare ground averaged over a 100m transect centered at nest		Sel, NS
res50	continuous	residual cover averaged over a 100m transect centered at nest		Sel, NS
perch	categorical	presence of perch site ≤75m or >75m from nest		Sel, NS
GIS data				
crop50	continuous	log ratio[a] crop:	5,4,16,22[b]	Sel, NS, Cor
tree50	continuous	log ratio tree:	5,4,16,22	Sel, NS, Cor
wet50	continuous	log ratio wetland:	5,4,16,22	Sel, NS, Cor
wat50	continuous	log ratio water:	5,4,16,22	Sel, NS, Cor
brgr50	continuous	log ratio sparse grassland:	5,4,16,22	Sel, NS, Cor
e.cp16	continuous	edge[c] of crop:	16, 22	Cor
e.tree16	continuous	edge of trees:	16, 22	Cor
e.dg16	continuous	edge of dense grassland:	16, 22	Cor
e.cp16L	categorical	edge of crop: 16. Low=L, Med=M, High=H		NS
crop16L	categorical	log ratio crop: 16. L<10%, M=10-30%, H=47-70%		NS
crbr16L	categorical	log ratio crop+sparse grassland: 16. L=20-34%, M=35-44%, H=45-70%.		NS

[a] Log ratio of (a_i /dense grassland).

[b] Radius of extent used: 5 = 50 m, 4 = 437 m, 16 = 1,600 m, 22 = 2,265 m.

[c] Edge density (edge/ha)

Table 2-2. Quasi-likelihood logistic regression explaining selection for sharp-tailed grouse nest sites in Alberta, 1999-2001. Habitat measured from ground surveys was modeled for nests from 2000 (n = 25) and 2001 (n = 33). Habitat measured with GIS data was modeled with nests surveyed from 1999-2001 (n = 67). Evidence for the strongest model (in bold) among those considered was evaluated with Akaike weights (ω_i).

Model	Constant	Explanatory variables	D[a]	n	k[b]	-2LL[c]	ΔAIC_c[de]	ω_i[fg]
50-m extent ground data 2000								
1	-5.11	+0.29 vor50	50.9	269	2	90.67	**0.00**	**0.660**
2	-5.71	+0.40 vor50 - 0.004 $vor50^2$	51.1	269	3	89.94	1.33	0.340
3	-0.81	- 0.46 bd50	7.5	269	2	170.19	79.51	0.000
4	-3.62	+0.48 res50	6.0	269	2	172.95	82.27	0.000
50-m extent ground data 2001								
5	-3.52	+0.39 vor50 - 0.01 $vor50^2$	20.9	258	3	204.76	**0.00**	**0.847**
6	-2.77	+0.19 vor50	17.7	258	2	212.24	5.42	0.056
7	-0.51	- 0.37 bd50	4.6	258	2	212.39	5.56	0.052
8	-3.07	+0.42 res50	4.4	258	2	212.73	5.91	0.044
50-m extent GIS data								
9B[h]	-4.11	+ 0.44 tree50 - 0.66 wet50	4.3	2853	3	732.03	**0.00**	**0.999**
10C[h]	-3.65	- 0.16 brgr50 - 0.02 crop50	1.5	2853	3	753.51	21.48	0.001
437-m extent GIS data								
11C[i]	-0.18	+ 0.28tree437 - 0.46 brgr437 - 0.03 crop437	3.3	163	4	213.48		

[a] Percent deviance explained by model (deviance full model/deviance null model).

[b] k is the number of variables, plus the constant, plus variance inflation factor ${}_c$ (Anderson and Burnham 2002).

[c] The –2log likelihood.

[d] Delta refers to the increase in AIC_c over the lowest observed value of AIC_c (Anderson et al. 2000). Subscript c refers to AIC corrected for small sample bias (Anderson et al. 2000).

[e] ΔAIC_c and Akaike ω_i are only comparable among models within the same group (model # 1-4, 5-8, 9&10).

[f] Estimated probability that model is the best among models considered (Anderson et al. 2000).

[h] C refers to candidate model. B refers to models derived from backward stepwise selection.

[i] Model obtained from backward stepwise selection was the same as the candidate model.

Table 2-3. Linear multiple regression explaining relative log density of crows and magpies related to landscape composition and edge at 2 spatial extents in Alberta, 2000 and 2001. Crows were counted at 26 landscapes and magpies at 25 landscapes. Akaike weights (ω_i) clarify the best model (in bold) within each extent for each species, and between extents for each species separately.

Model	Spp.[a]	Constant	Explanatory variables		R^2	k[b]	RSS[c]	ΔAIC_c[d]	ω_i	ΔAIC_c	ω_i
								Within[e] extents		Between[e] extents	
1600-m extent											
1	c	+1.61	+ 0.29 brgr16	- 0.01 e.dg16	31.7	4	2.25	**0.00**	**0.312**	**0.00**	**0.184**
2	c	+0.67	+ 0.15 brgr16	- 0.01 e.tree16	26.0	4	2.44	0.88	0.201	0.88	0.119
3	c	+0.66	+ 0.07 crop16	- 0.01 e.tree16	25.7	4	2.45	0.95	0.194	0.95	0.114
4	c	+1.40	+ 0.05 crop16	- 0.01 e.dg16	23.4	4	2.53	1.29	0.164	1.29	0.097
5	c	+0.39	+ 0.09 crop16	+ 0.21 brgr16	10.3	4	2.96	3.08	0.067	3.08	0.039
6	c	+0.12	+ 0.11 crop16	- 0.20 tree16	8.8	4	3.01	3.26	0.061	3.26	0.036
2265-m extent											
7	c	+0.79	+ 0.34 brgr22	- 0.01 e.tree22	28.0	4	2.38	**0.00**	**0.331**	0.60	0.136
8	c	+1.79	+ 0.50 brgr22	- 0.01 e.dg22	22.7	4	2.55	0.81	0.221	1.40	0.091
9	c	+0.72	+ 0.06 crop22	- 0.01 e.tree22	21.0	4	2.60	1.04	0.197	1.64	0.081
10	c	+0.40	+ 0.09 crop22	+0.36 brgr22	10.9	4	2.94	2.41	0.099	3.01	0.041
11	c	+1.20	+ 0.05 crop22	- 0.01 e.dg22	7.8	4	3.04	2.79	0.082	3.39	0.034
12	c	+0.13	+ 0.13 crop22	- 0.20 tree22	4.9	4	3.14	3.15	0.069	3.74	0.028
1600-m extent											
13	m	-0.12	+ 0.13 brgr16		3.1	3	2.00	**0.00**	**0.317**	0.04	0.158
14	m	-0.13	+ 0.05 crop16		2.0	3	2.02	0.12	0.298	0.16	0.149
15	m	-0.29	+ 0.14 brgr16	+0.004 e.cp16	14.0	4	1.77	1.52	0.148	1.56	0.074
16	m	-0.10	+ 0.05 crop16	+0.12 brgr16	4.6	4	1.97	2.69	0.083	2.73	0.041
17	m	-0.05	+ 0.11 brgr16	+0.07 tree16	3.7	4	1.99	2.79	0.079	2.83	0.039
18	m	-0.19	+ 0.06 crop16	+0.002 e.tree16	3.0	4	2.00	2.86	0.076	2.91	0.038
2265-m extent											
19	m	-0.12	+ 0.11 crop22		3.5	3	1.99	**0.00**	**0.321**	**0.00**	**0.161**
20	m	-0.11	+ 0.17 brgr22		3.0	3	2.00	0.05	0.313	0.05	0.157
21	m	-0.30	+ 0.19 brgr22	+ 0.004 e.cp22	11.6	4	1.82	1.90	0.124	1.90	0.062
22	m	-0.08	+ 0.10 crop22	+ 0.15 brgr22	5.7	4	1.94	2.60	0.088	2.60	0.044
23	m	-0.16	+ 0.12 crop22	+0.001e.tree22	3.7	4	1.99	2.84	0.078	2.84	0.039
24	m	-0.06	+ 0.20 brgr22	+ 0.06 tree22	3.3	4	1.99	2.88	0.076	2.88	0.038

[a] Response variable used in model: c = log(crow/km^2), m = log(magpie/km^2).

[b] k is number of explanatory variables, plus constant, plus variance term (Anderson et al. 2000).

[c] RSS is the residual sum of squares (Anderson et al. 2000).

[d] Delta refers to the increase in AIC_c over the lowest observed value of AIC_c (Anderson et al. 2000). Subscript c refers to AIC corrected for small sample bias (Anderson et al. 2000).

[e] Within and Between extents: For example, crow models compared within the 1,600-m extent include models 1–6. Crow models compared between extents include models 1–12.

Table 2-4. Quasi-Likelihood logistic regression explaining nest success (n = 67) with habitat at multiple extents for sharp-tailed grouse in Alberta, 1999–2001.

								Step 1[a]		Step 2[b]		Step 3[c]	
Model	Constant	Explanatory variables	Extent	Data	D[d]	k[e]	-2LL	ΔAIC_c[f]	ω_i[g]	ΔAIC_c	ω_i	ΔAIC_c	ω_i
1C	-1.11	+ 0.05 vor2	2	ground	4.6	3	88.51	**0.00**	**0.724**	11.25	0.002	17.10	0.000
2C[hi]	-0.16	+ 0.07 vor2 - 0.002vor2^2	2	ground	5.0	4	88.10	1.93	0.276	13.19	0.001	19.03	0.000
3C[i]	-1.82	+ 0.19 vor50	50	ground	15.6	3	77.26	**0.00**	**0.700**	**0.00**	**0.694**	5.85	0.036
4C	-1.72	+ 0.16 vor50 + 0.001vor50^2	50	ground	15.6	4	77.24	2.25	0.228	2.25	0.226	8.09	0.012
5C	-1.77	+ 0.15 vor50 + 0.002 vor50^2-0.40 perch	50	ground	17.8	6	75.24	5.00	0.057	5.00	0.057	10.85	0.003
6C[i]	-0.55	- 0.34 crop50	50	GIS	3.7	3	89.45	**0.00**	**0.880**	12.19	0.002	18.04	0.000
7C	-0.19	- 0.03 tree50 - 0.17 brgr50	50	GIS	1.8	4	91.16	3.98	0.120	16.17	0.000	22.02	0.000
8C	-0.09	- 0.28 crop437 - 0.58 brgr437 + 0.57 tree437	437	GIS	11.0	5	82.53	**0.00**	**0.625**	9.87	0.005	15.72	0.000
9C[i]	-0.55	- 0.28 crop437	437	GIS	5.0	3	88.15	1.02	0.375	10.89	0.003	16.74	0.000
10C[i]	+0.23	+2.02 crbr16L + 1.05 crbr16M	1600	GIS	12.2	5	81.44	**0.00**	**0.967**	8.78	0.009	14.63	0.000
11C	+0.25	+ 0.92 crop16L - 0.98 crop16M	1600	GIS	8.8	5	84.61	3.17	0.198	11.95	0.002	17.80	0.000
12C	+0.05	+ 0.75 e.cp16L + 0.27 e.cp16M	1600	GIS	4.9	5	88.19	6.76	0.033	15.54	0.000	21.38	0.000
Best model all extents, GIS and ground													
13C	-2.98	+0.25 vor50 + 1.18crop16L -1.99crop16M	50,1600	ground,GIS	29.6	6	64.39	**0.00**	**0.717**			**0.00**	**0.665**
14B	-2.85	+ 0.21 vor50 - 0.36 crop437	50,437	ground,GIS	22.5	4	70.86	1.71	0.305			1.71	0.263
15C	-1.46	+ 0.05 vor2 + 0.81 crop16L -1.14 crop16M	2,1600	ground,GIS	13.0	6	80.69	16.30	0.000			16.30	0.000
Best model all extents GIS data alone													
16B	+0.98	+0.60 tree437 +2.04crbr16L +0.92crbr16M	437,1600	ground,GIS	16.5	6	77.46					13.07	0.001

[a] Step 1 evaluates best model within each extent and survey method (e.g. models compared with GIS data at 1,600-m extent include models 10–12C).

[b] Step 2 evaluates the best model among all extents and survey methods (i.e. models under consideration includes 1–12C).

[c] Step 3 evaluates the best overall model (i.e. models under consideration among all extents and survey methods including 1–16B).

[d] Percent deviance explained (deviance full model /deviance null model).

[e] k is the number of variables, plus the constant, plus the variance inflation factor $_c$ (Anderson and Burnham 2002).

[f] $\Delta_i = AIC_i$ - minAIC (Anderson et al. 2000: 918). Subscript c refers to AIC corrected for small sample bias (Anderson et al. 2000).

[g] Evidence for strongest model evaluated with Akaike weights ω_i.

[h] C refers to candidate models. B refers to models derived from backward stepwise selection.

[i] Identifies where the model selected by backward stepwise selection is the same as the candidate model.

Table 2-5. Quasi-Likelihood logistic regression explaining nest success (n = 67) with an interaction between concealment cover and the presence of perch sites ≤ 75 or > 75 m from nests in a post hoc analysis for sharp-tailed grouse in Alberta, 1999–2001. Evidence for the strongest model was evaluated with Akaike weights (ω_i).

Model	Constant	explanatory variables	D^a	k^b	$-2LL^c$	$\Delta AIC_c{}^d$	ω_i
1	-2.52	+ 1.04 perch>75 + 0.21 vor50*perch≤75 + 0.20 vor50*perch>75	20.4	6	68.345	**0.00**	**0.999**
2	-1.28	- 0.04 perch>75 + 0.04 vor2*perch≤75 + 0.07 vor2*perch>75	8.0	6	82.732	14.39	0.001

[a] Percent deviance explained (deviance full model /deviance null model).

[b] k is the number of variables, plus constant, plus variance inflation factor $_c$ (Anderson and Burnham 2002).

[c] The –2log(likelihood).

[d] Delta refers to the increase in AIC_c over the lowest observed value of AIC_c. Subscript c refers to AIC corrected for small sample bias (Anderson et al. 2000).

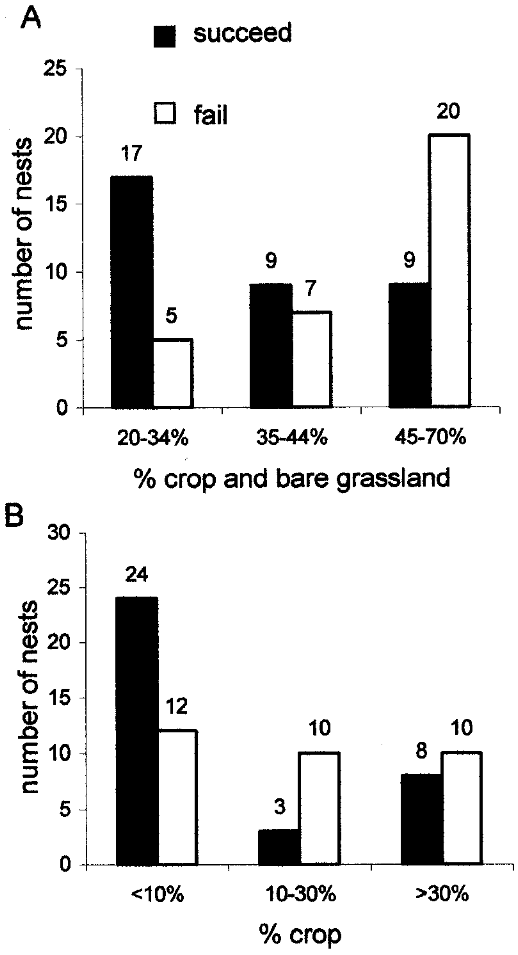

Fig. 2-1. Sharp-tailed grouse nests (n = 67) in landscapes characterized by the proportion of (A) sparse grassland and crop, and (B) crop alone within a 1,600 m extent in Alberta, 1999–2001. Numbers above bars indicate numbers of nests.

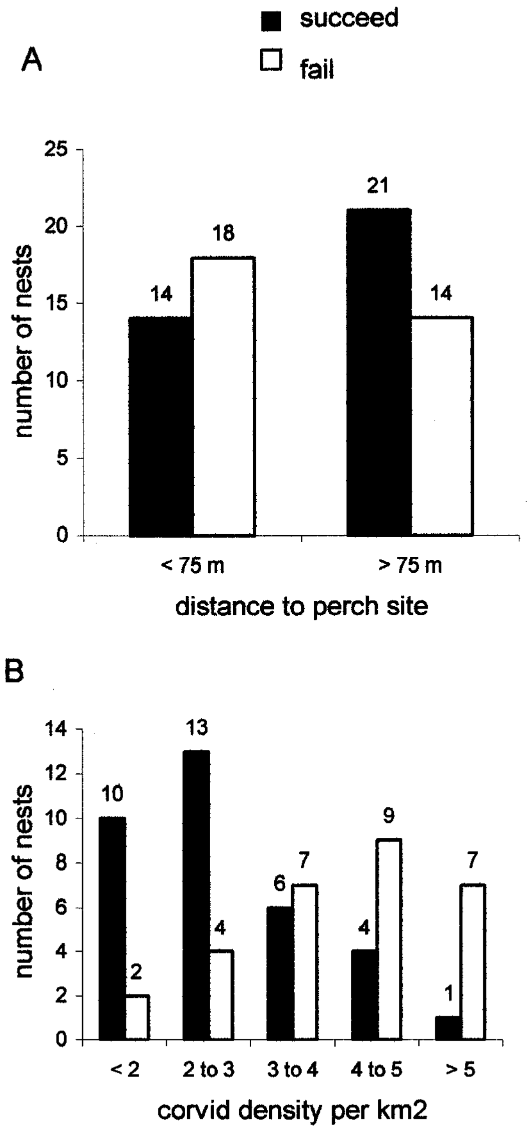

Fig. 2-2. Sharp-tailed grouse nest success (n = 67) in relation to A) distance from the nearest potential predator perch site, and B) corvid density measured at the 1,600-m extent. Numbers above bars indicate numbers of nests.

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CHAPTER 3

GROUSE BROOD SUCCESS AND RAPTOR DENSITY IN RELATION TO HABITAT

INTRODUCTION

Breeding success for ground dwelling birds has been associated with human related land use at landscape spatial scales. The proportion of female grouse with broods was negatively related to the amount of crop and pastureland at broad scales in Scandinavia (Kurki et al. 2000), and to heavily grazed areas in Britain (Baines 1996, Calladine et al. 2002). These studies highlighted that land use is associated with breeding success for grouse; however, because they did not follow individual hens, they could not pinpoint at what reproductive stage most mortality occurred. Precocial young for many ground dwelling birds experience high mortality during the initial 1-3 weeks post-hatch (Flint et al. 1995, Korschgen et al. 1996, Riley et al. 1998). Hence, studies that use flush counts on non-marked hens cannot distinguish if differences in brood success among land use regimes are a function of nest success, early brood mortality, or a combination of the 2. Clarity on this point is important for understanding the life stage most relevant for affecting change in population density. It is also important for clarifying which predators are most affecting population density in a particular system.

While changes in habitat may be the ultimate cause of decline for prairie grouse (Schroeder and Robb 1993, Connelly et al. 1998, Giesen 1998, Schroeder et al. 1999), predators are the proximate cause of mortality for most individuals (Schroeder and Baydack 2001). The density, composition, and searching efficiency of predators are affected by habitat structure and composition. At broad extents, fox (*Vulpes vulpes*) density in Finland (Kurki et al. 1998) and corvid density in Sweden (Andrén 1992) was greater in forested landscapes fragmented by crop and pastureland. At smaller extents, changes in habitat that reduce concealment from predators, or force prey to group spatially, can aid the efficiency of predators (Gates and Gysel 1978, Smedshaug et al. 2002). Lower concealment cover has been associated with greater predation on both nests and broods for grouse in a number of areas (Lutz et al. 1994, Baines 1996, Wiebe and Martin 1998). Understanding how predators are affected by human related changes in habitat is important for managing birds and other species vulnerable to the dynamics of predators (Ormerod 2002).

Natural prairie systems have been dramatically altered by fire suppression, fragmentation by agriculture, and degradation of grasslands from stock grazing (Johnson and Winter 1999). I studied habitat use and success for sharp-tailed grouse (*Tympanuchus phasianellus*, hereafter sharp-tails) broods up to 30-days post-hatch in the prairies of southern Alberta. My intention was to investigate how human changes in habitat altered the dynamics between predator and prey. I did this indirectly by measuring habitat at multiple extents relevant to broods and raptors. Four objectives guided this work. The first was to identify the habitat used by broods in the first week post-hatch. I predicted broods would select areas with concealment cover height best described by an inverted U quadratic relationship: i.e. they would avoid very open areas where predators might see them and would avoid densely vegetated areas where they may be unable to detect or escape predators (Wiebe and Martin 1998). I predicted selection for mesic areas that would provide good concealment cover and important food resources (insects, forbs) for chick growth (Aldridge and Brigham 2002). I predicted selection for willow and tree patches that presumably provide shade during mid-day (Moyles 1981). Second, I determined the spatial extent and habitat that best predicted raptor density. Third, I determined the habitat characteristics associated with brood success at 2 extents: that relevant to the habitat used by broods and that relevant to the habitat used by raptors at the landscape scale. Fourth, I examined if broods hatched earlier in the season were more likely to survive. Limited evidence suggests precocial broods hatched late in the season have lower survival, possibly due to the extra energy spent by hens during re-nests or diminishing habitat quality (i.e. less concealment cover after hay cut, Riley et al. 1998, Rotella and Ratti 1992).

STUDY AREA

The study occurred in an area of 1,392 km^2 in the Mixed Grass Prairie of southeastern Alberta (51°45'N and 111°W). The area included a broad variation in the amount of perennial grassland disturbed by conversion to agriculture crops at landscape extents. Topography was predominately flat with moderate rolling hills towards the southeast. Prominent grasses were fescue (*Festuca* spp.) and needle and thread (*Stipa comata*), and common shrubs included western snowberry (*Symphoricarpos occidentalis*), prairie rose (*Rosa* spp.) and willow (*Salix* spp.). Tree cover was patchy with pockets of aspen (*Populus tremuloides*) found in depressions, along north slopes and around homesteads, but wider encroachment was evident across the matrix. The primary land use was cattle ranching, followed by agricultural crops (wheat, canola, pea). Oil and gas extraction occurred in clusters across the region. Long term precipitation averaged 371 mm per annum in this region (Appendix 2).

METHODS

Sharp-tail hens were captured annually in late April from 1999–2001, prior to nesting, using walk-in funnel traps (Toepfer et al. 1987) at 10–16 leks. Hens were fitted with a 14-g necklace radio collar (Holohil Systems, Carp, Ontario, Canada), and located with a portable receiver and 3-element yagi antenna every 5-days during brood rearing to 30-days post-hatch. Nests were considered successful if ≥1 chick hatched. Hens were triangulated from approximately 30 m to avoid disturbing broods. A brood was considered successful if at least 1 chick was alive at day-30. Broods were flushed at day 30 by searching in a systematic pattern over a 100-m radius around the hen. Flush counts are inherently biased towards under estimating chick survival because some chicks that are alive do not flush. It is also probable that the reliability of flushing the same proportion of chicks in a brood will vary based on the structure of the vegetation. Chicks become harder to find and flush as vegetation height and density increases. However, flush counts are useful as an index of brood success (1 = ≥ 1chick alive, 0 = no chicks alive) because it is quite easy to distinguish if the hen has at least 1 chick. Additionally, hens that have lost their entire brood tend to flush long distances (i.e. > 400 m) without returning to the flush location. They also tend to flush at greater distances from the investigator when approached. In contrast, hens with broods often allow the researcher to approach much closer before flushing (< 30 m), and generally fly shorter distances (personal observation). Moreover, hens with broods tend to move back near to the flush location within 10-20 min. Distraction displays are also common, but these tend to diminish as chicks get old enough to fly longer distances. Therefore, it is generally quite easy to assess if a hen still has a brood at 30-days post-hatch. I considered a brood successful if ≥ 1 chick was flushed. If the hen acted broody (returned near to the area of flush) but chicks were not found, I returned on the next day to flush again. I searched for lost hens during nesting and brood rearing with a fixed-wing aircraft intermittently through the summer.

Habitat Data

Ground Surveyed Data.—To avoid disturbing the brood or altering movement behavior, habitat data were surveyed on the day after locating a brood, or the nearest day to that date once the brood had left the immediate area. Concealment cover was estimated with a visual obstruction reading pole (Robel et al. 1970) read from 2 m away. Readings were averaged at 10-m intervals along a 100-m east-west transect. An estimate of bare ground and residual cover was averaged over 3 measurements along the transect using 20 X 50-cm Daubenmire plots. Shrub density was estimated over a 100-m radius into low (scarce individual shrubs), medium (1 or more patches of shrub) and high (continuous dense shrub) categories. Table 3-1 includes a summary of explanatory variable coding and the analyses used.

GIS Surveyed Data.—Habitat composition was estimated with the GIS program Arcview 3.2 (Environmental Systems Research Institute, Inc.) using a Landsat 7 image taken in 1999 at 30 X 30-m resolution. These data were classified using the program PCI Geomatica 8.2 (PCI Geomatics). Aerial photos (1:30,000) and ground truthing were used to improve the accuracy of classification. Accuracy ranged between 80-94.8% for each class with an overall rating of 85.6% (K_{hat}), based on stratified random ground truthing (Jensen 1996).

The composition of habitat across the study area was categorized into 6 classes: dense grassland (39%), sparse grassland (27%), crop (26%), trees (4%), wetland (2%) and water (2%, Table A-3-1). Dense grassland included areas with perennial grasses and shrub cover. Sparse grassland included areas with perennial grass and shrub cover, but had more bare ground reflectance than dense grassland. I used ground surveyed data to calibrate the classification for sparse grassland based on Daubenmire readings with more than 25% bare ground. Sparse grasslands were presumably affected by soil type and/or heavy stock grazing over a period of years. Evidence for the relative influence of grazing was anecdotal based on personal communication with landowners and the regional range manager. Crop included cultivated land, hay land, and anthropogenic disturbance (homesteads, country roads). I included all tree species and tall willows in 1 category that I defined from ground truthing as woody vegetation over 3 m in height. The density of edge/ha was calculated for habitat classes using the Patch Analyst extension in Arcview 3.2. (Elkie et al. 1999).

Habitat composition from the 6 classes summed to 100% and therefore the covariates were not independent when treated as continuous variables (Aebischer et al. 1993). I used log ratios [i.e. $\log(a_i/b)$] to remedy this problem (Aebischer et al. 1993, Kurki et al. 1998) by using dense grassland as the denominator (b) for the remaining 5 classes (a_i). The interpretation was expressed as the influence of habitat a at the expense of habitat b (Kurki et al. 1998). Dense grassland was used as the reference category because it was the most abundant cover class. I replaced zero values with 0.001 to make log ratio transformations possible (Aebischer et al. 1993). Log ratio explanatory variables included the relative proportion of crop, sparse grassland, trees, wetland, and water (Table 3-1).

Potential Brood Predators

Potential predators of chicks included raptors, mammals and possibly corvids. Raptors in the region included red-tailed hawk (*Buteo jamaicensis*), northern harrier (*Circus cyaneus*), Swainson's hawk (*Buteo swainsoni*), ferruginous hawk (*Buteo regalis*), great horned owl (*Bubo virginianus*). Coyotes (*Canis latrans*) were common in the region, with rare evidence of the presence of red fox (*Vulpes vulpes*), skunk (*Mephitis mephitis*), and badger (*Taxidea taxus*). Possible corvid predators in the region included American crow (*Corvus brachyrhynchos*) and black billed magpie (*Pica pica*).

To estimate how raptor density varied with habitat, surveys were conducted twice per year in late May and again in late June or early July in 2000 and 2001. Point counts were made from 0.5 hr before sunrise to 3 hrs after sunrise along 26 3,200-m transects with 5 stations 800 m apart. Transects were randomly located in habitat stratified by the proportion of crop at a 1,600-m extent to ensure surveys were conducted along a gradient of cropland landscapes. Birds of prey seen or heard at stations and between stations within a 400 m radius were recorded and summed over the transect. Habitat was measured within 1,600 m and 2,265 m buffers centered at the 1,600-m mid-point of the transect. Transects were a minimum of 4,530 m apart (2,265 m x 2) to avoid double counting the habitat.

Spatial Scale

Spatial scales relevant to the brood ecology of sharp-tails were considered for 2 processes including 1) the habitat selected by hens for rearing broods, 2) the extent affecting the density of likely avian brood predators. On the ground, vegetation data were collected at random points within 1,600 m of leks in 2000 and 2001 to characterize available habitat. I based this distance on descriptions of habitat use from the literature (Giesen and Connelly 1993). Nearly all broods were within 1800 m of the nearest lek (95% CI, n = 40), so I used this distance as the extent of habitat available for brood rearing around the 16 capture leks for analysis with GIS data. I also considered habitat available for brood rearing across the region. I did this by generating random points within a 100% minimum convex polygon of the leks with 1 or more broods across the study area (1,088 km^2).

There were not enough locations during brood rearing from day 1 to 30 to estimate brood home range reliably using minimum convex polygons (MCP). Instead, I approximated the extent of habitat used during this period by measuring the distance from the location on day 5 to all other locations up to day 30. This was accomplished with a GIS using universal transverse mercator (UTM) readings taken from hand-held GPS units. I used day 5 as the mid-point for measuring distance to brood locations since precocial broods commonly move hundreds of meters from the nest within the first few days after hatch (Riley et al. 1998). Nearly all locations were within 583 m of the day 5 location (95% CI, n = 30 broods) so I used a radius of 583 m around this location to measure habitat use during brood rearing. This area (106.7 ha) is within the range of habitat used by sharp-tail hens over the breeding season in southwestern

Alberta in 1998 and 1999 (Roersma 2001, 20.3 to 195.8 ha, $\bar{x} = 69.12$ ha). On a smaller scale, I considered habitat use within 50 m of brood locations. The 50-m scale allowed me to use both ground surveyed habitat information and data analyzed with a GIS. This smaller extent (50 m) was evaluated because I presumed brood habitat selection could occur at this scale and that predators searching for broods could use habitat cues at this scale.

I modeled relative raptor density by habitat composition and edge density measured at 1,600 m and 2,265 m scales to identify the extent most relevant for describing avian predator density. I then used habitat from this extent to model grouse brood success. I do not know the territorial size for raptors in this region, but based on other studies I estimated that ≥ 1 pair would be found in landscapes of 8 km^2 (1,600-m radii). The density of nesting female harriers ranges from 0.06 to 0.82 km^2 for dry grasslands and farmland (Potts 1998). Distance estimates between nests typically range from 1.5–2.5 km for Swainson's hawk (England et al. 1997) and 2.3 km between nests for Ferruginous hawks (Gilmer and Stewart 1983). Home range estimates for Great horned owls commonly range from 0.70–4.83 km^2 (Houston et al. 1998).

Analyses

Akaike's Information Criteria corrected for small sample bias (AIC_c), was used to calculate Akaike ranks (ΔAIC_c) and weights (ω_i) to identify models with the most evidence for fitting these data (Anderson et al. 2000, Anderson and Burnham 2002). The ω_i estimated a probability that a given model was the best among those considered (Anderson et al. 2000). Describing the approximate likelihood of model *i* being better than model *j* was derived by ω_i / ω_j. Odds ratios were used to interpret logistic regression results (i.e. $e^{\text{beta coeff}}$), and for comparing the ratio of odds between 2 groups of binary data (Ramsey and Schafer 2002: 538). The amount of deviance explained (D, logistic regression: deviance full model/deviance null model) or R^2 (linear regression) were used as a descriptive measure of how well models fit the data (Menard 1995, Ramsey and Schafer 2002). Data were checked for influential cases with leverage ratios and studentized residuals (Menard 1995). I used correlation matrices to identify and remove redundant variables before fitting regression models (Ramsey and Schafer 2002). Where backward stepwise regression was used, alpha values were set at 0.05 for removal and entry of covariates. Regression procedures using categorical explanatory variables required 1 category be removed, hence I used the last category as the reference. Means are reported with standard errors (SE). Statistical analyses were performed with SPSS 11.0 (SPSS Inc.) and Statistica (StatSoft, Inc.) software.

Brood Habitat Selection.—I defined *a priori* candidate models for brood habitat selection based on my predictions of how the system worked. Since knowledge of the system was imperfect, I also built stepwise regression models for comparison with candidate models. At small scales with habitat measured from ground surveys, I predicted that broods would use areas with more concealment cover than available at random on the landscape {vor50; shrubL}. I also looked for an inverted U quadratic function with concealment cover because hens may avoid sparse cover, and very dense cover if it hindered their ability to detect predators {vor50+vor50^2}. I predicted that broods would use locations closer to tall willows or trees than randomly available {perch<75}(Moyles 1981).

For the GIS habitat data, I predicted that broods would use mesic areas that were surrounded by willows and trees because I assumed these areas would provide cover and insects important for early chicks (Moyles 1981, Aldridge and Brigham 2002, Richard et al. 2002) {wet50+tree50; wet583+tree583}. I predicted broods would avoid areas with more sparse grassland than available at random because it probably offers less concealment from predators {brgr50; brgr583}. I also predicted broods would avoid areas with greater proportions of crop {crop583} assuming these habitats provide poor concealment cover.

I modeled habitat use vs. availability separately for each extent (50 m, 583 m) and for ground vs. GIS surveyed data. Use data was based on brood locations at day 5, or the last known location for broods that did not survive to day 5. Models were derived using quasi-likelihood logistic regression (Anderson and Burnham 2002). I assumed samples lacked spatial independence at some extent, and therefore applied the quasi-likelihood approach to inflate the standard error (SE) for beta coefficients (Anderson et al. 2000, Ramsey and Schafer 2002). As previously described, the extent of available habitat was 1,600 m for ground surveyed data, 1,800 m and 1,088 km^2 for GIS data. I compared candidate models at each extent with models determined from backward stepwise regression. Model comparisons using ΔAIC_c and ω_i were not made between extents nor between data from different years or survey methods because use and availability differed among these subsets (Anderson and Burnham 2002). Comparisons with ΔAIC_c and ω_i were performed within each subset.

Predator Density and Spatial Extent.—Least squares multiple linear regression was used to evaluate the most relevant extent for explaining bird of prey density with habitat covariates. Model development was conducted in 4 stages. First, I viewed the data graphically with scatter plots to detect non-linear relationships between explanatory variables and raptor density. Non-linear terms were included as covariates where identified. Second, a correlation matrix was used to assess bivariate relationships between habitat variables and raptor density that could then be used in models performed with least squares multiple linear regression. The matrix also helped me to identify and avoid using highly correlated habitat variables (Pearson Correlation) in the same model. Influential observations (outliers) were examined using Cooks distance and Leverage values (Ramsey and Schafer 2002). Third, I examined if raptor density should be analyzed for each year separately or averaged for each transect separately between years by looking for a year effect in initial models. I modeled density with year and the habitat covariate with the strongest correlation (Andrén 1992). Fourth, linear regression models were used to evaluate the most relevant extent for explaining raptor density with habitat covariates. No more than 2 explanatory covariates were used in the same model to avoid over-fitting these data given the moderate sample size ($n \approx 25$). Residuals were plotted with predicted values and normal probability plots to evaluate assumptions of equal variance and normality (Ramsey and Schafer 2002). The extent having the model with the highest ω_i was considered the best spatial scale for explaining raptor density.

Brood Success and Habitat.—Brood success was analyzed in 5 steps using quasi-likelihood logistic regression. In the first step, the best model for describing brood success with habitat data was determined within each extent (583 m and 1,600 m) by comparing univariate models with ω_i. At the 583-m scale, I compared these models with the 1 selected via a backward selection procedure because knowledge of the habitat associated with brood rearing success is not well known. At the 1,600-m scale, habitat composition and edge density were based on measurements centered at the nearest lek and categorized into low, medium and high based on patterns in the data (Table 3-1). A backward selection procedure was not used at the 1,600-m extent because I did not want to over-fit these data given the sample size ($n = 40$) available for these categorical variables. I included a covariate that aggregated crop and sparse grassland at the 1,600-m scale {crbr16L, Table 3-1}, because this variable was negatively associated with nest success for sharp-tails (Chapter 2). In the second step, I identified the best extent for describing brood success by comparing the Akaike ω_i from the suite of models developed in step 1. Third, I modeled brood success by hatch date. Fourth, the best overall model was derived by applying backward stepwise regression using potential habitat variables from the top models within each extent (step 1) and hatch date ($n = 4$ covariates), and from a full model using these same covariates except hatch date ($n = 3$ covariates). As a final step, I looked for strong interactions using year and hatch date separately with habitat covariates from the best models in step 4. Models with interactions were reported if ΔAIC_c values were ≤ 2 compared with the models in step 4 (Anderson and Burnham 2002).

The sample of hens was captured at 16 leks across the region. Given that nearly all brood locations were found within 1,800 m (10.19 km^2) of a lek, their distribution was somewhat clumped at a regional scale. However, most organisms are clumped at some spatial extent (Wiens 1989), hence we need to balance assumptions of independence with practical data collection limitations. I considered hens and therefore broods located near the same lek to be individual sample units because; 1) all hens attempted to nest, which implied space was not limited on the landscape, 2) hens were not dependent on males for breeding territories and therefore selected brood rearing habitat based on individual preference.

I reduced the likelihood of pseudoreplication between brood locations due to spatial correlation or individual hen behavior by limiting the sample of broods to 1 per hen. If hens reared broods in more than 1 year, I randomly selected 1 brood for that hen. I also limited the sample by randomly removing 1 or more broods within 1,166 m (2 x 583 m = 1,166 m) of the next closest brood based on locations on day 5. At the 1,600-m extent, habitat data used by 2 or more broods overlapped in some cases. Thus, standard errors and therefore confidence intervals for the beta coefficients of 1,600-m covariates may be underestimated even though I used the scaling mechanism that inflates SE via the quasi-likelihood procedure (Anderson et al. 2000, Ramsey and Schafer 2002). To avoid misleading the reader, I treated 1,600-m scale habitat covariates as categorical (Table 3-1) and ensured that each habitat category had broods from at least 3 different leks to represent patterns in a number of these 8 km^2 landscapes.

RESULTS

Brood Survival

Forty-nine hens had 1 or more successful nests over 3 years for a total of 57 brood rearing events. One hen and brood were lost and fate could not be determined. Normally hens did not re-nest after losing a brood, however, in 2001 1 female hatched her clutch and lost the entire brood (presumabley predation) on the first day. She proceeded to lay and hatch a second clutch in the same season. Thirty-two broods (57%) had at least 1 chick survive to 30 days. Hence, 25 broods experienced 100% mortality within 30 days (assuming no brood mixing) with the hen killed for 9 of those broods. Flush counts at 30 days post-hatch showed an average of 2.14 ± 0.35 (95% CI 1.46–2.82) chicks/brood based on the sample of 56 known brood events. This average increased to 3.81 ± 0.42 (95% CI 3.06–4.68) chicks/brood when the denominator was based on 32 successful broods. Seasonal rainfall was greater than average in 1999, and lower than average in 2000 and 2001 (Appendix 2 Fig. A-2-1).

Brood Habitat Selection

I used 18 broods in 2000 and 25 in 2001 to model early habitat selection with ground data at the 50-m extent. Random ground survey data was not collected at the landscape extent in 1999, so I did not include broods from 1999 in this analysis. Years were modeled separately because available habitat data corresponded with use data in a single year. Available habitat was measured at 240 and 218 random sites in 2000 and 2001 respectively.

For ground surveyed data, early brood habitat selection was best described by the height of concealment cover within 50 m of brood locations in both years (Table 3-2; data range Table A-3-4). In general, broods used areas with more concealment cover than available at random. However, the shape of the function changed between years and was best described as linear in 2000 and non-linear in 2001 (inverted U, models 1C and 6C respectively, Table 3-2). The explanatory ability of concealment cover varied by nearly an order of magnitude between years, explaining 4 and 29% of the deviation in habitat selection for broods in 2000 and 2001.

I used 40 locations from individual broods from 1999 through 2001 to model habitat selection with GIS measured habitat data. The number of random points for measuring available habitat was 1,170 at the 50-m extent and 65 at the 583-m extent. Strength (ω_i) was similar among models at the 50 m extent, with a negative association with wetland and sparse grassland, and a positive association with treed habitat (models 9C, 10C and 11B, Table 3-2). Evidence at the 583 m extent was more conclusive with broods demonstrating avoidance for areas with more sparse grassland (models 13C, Table 3-2). The relative fit of models derived from GIS variables was low at 50 and 583 m extents with the best model from either scale explaining less than 4 % of the deviation (Table 3-2).

The proportion of deviation explained by GIS variables improved when using random available habitat across the region rather than within 1,800 m of the nearest lek. I used a sample of 500 random available points at the regional scale. The best model at this scale included a positive association with treed habitat, and a negative association with sparse grassland and crop at the expense of dense grassland (Model 16C, Table 3-2). The model including these 3 variables explained 10% of the deviation in brood habitat selection across the region.

Predator Density and Spatial Extent

The average density of raptors was 0.50 / km^2 ± 0.05 over the 2-years. I averaged raptor density over 2 years because YEAR was not statistically significant when examined in preliminary models (linear regression with t values representing a year effect: 1,600 m, $t = -1.76$, $P = 0.08$; 2,265 m, $t = -1.79$, $P = 0.08$). The relationship between sparse grassland and raptor density appeared non-linear in scatter plots, so a quadratic term for this covariate was added to the pool of explanatory variables. When examining the data for influential observations, 1 case was deemed an outlier and subsequently removed thereby reducing the sample size to 25 landscapes.

Evidence of relative strength (ω_i) was spread over ≥ 2 models when compared within and between the spatial extents used in relating raptor density with habitat. Wetland and sparse grassland both demonstrated strong relationships with raptor density at 1,600 and 2,265-m scales (data range Table A-3-5). The function with sparse grassland was best described as a quadratic (Fig. 3-1), with raptor density decreasing at low and high levels. Wetland edge and wetland were both positively associated with raptor density (Table 3-3), indeed there was no difference in the ω_i between models using these competing covariates at the 1,600-m extent. Moreover, wetland covariates became increasingly important as the scale of measure increased from 1,600 to 2,265 m (models 1 and 10, 5 and 14, Table 3-3).

Landscape variables explained up to 36% of the variation in raptor density, with the non-linear relationship with sparse grassland having moderate support as the best overall model (model 8, Table 3-2). This model was 1.3 times (ω_i/ω_j) more likely to be better for explaining raptor density than the top model from the 2,265-m extent (wetland edge, model 10, Table 3-3). Hence, I used the 1,600-m extent as the scale most relevant for relating brood success with broader scale habitat.

Brood Success and Habitat

There were 40 non-overlapping broods based on locations at day 5 (2 x 583 m = 1,166 m). Hence, I used this sample of 40 broods to estimate success in relation to habitat. Brood success was negatively associated with the proportion of crop and sparse grassland at 583 m and 1,600-m extents (Fig. 3-2A and 3-2B). These 2 covariates had moderate support as the best model for describing brood success at the 583-m scale (step 1), and for the best overall model from all potential covariates (step 2 and step 4) (models 5B and B19, Table 3-4). These 2 habitat variables explained 13% of the deviation in brood success. Models demonstrating a negative relationship between wetland and brood success had moderate support at the 1,600 m extent, and indeed a model using this variable was the strongest single model at this broader extent (model 8, Table 3-4). Hence, moderate support suggests broods were more likely to succeed in landscapes with less wetland compared with those in areas with more wetland (model 8, Table 3-4). The overall proportion of wetland was relatively low across the study area ranging from 1–9% of the habitat within 1,600-m landscapes.

Brood success appeared to be greater in landscapes with $\leq$0.75 raptor/km^2 when viewed graphically (Fig. 3-3), but there was no evidence that the relationship was statistically significant (odds ratio, 95% CI 0.27–17.57). Moreover, hatch date was not associated with brood success (model C1, Table 3-4, step 3), nor did I find a strong interaction between year or hatch date and the habitat variables for either extent (step 5). The ΔAIC_c values for these interactions were greater than 3 in all cases when compared against models in step 1 and 4.

DISCUSSION

Brood Survival

Brood success (57%) was relatively high in this area compared with the limited number of similar studies on prairie grouse in northern latitudes. Sharp-tail brood success averaged 32% over 2 years in southwestern Alberta (Roersma 2001), 48% over

2 years in Montana (Bousquet and Rotella 1998), and 42% over 2 years for sage grouse (*Centrocercus urophasianus*) in southeastern Alberta (Aldridge 2000). My estimate of brood success occurred over 30 days, which is a shorter period than at least 2 of these 3 studies (50-d, Aldridge 2000; 54-d, Bousquet and Rotella 1998; unspecified, Roersma 2001). However, 73% of the chick mortalities occurred within 15 days post-hatch in this study implying that the rate of survival increases as chicks grow older (Chapter 4). Therefore, hens appear to be comparatively successful in rearing broods in this system, notwithstanding the shorter period used to evaluate brood success.

A similar portion of hens entering the breeding season successfully reared a brood in each of the 3 recent studies on prairie grouse in Alberta (29% current study; 18% and 28% over 2 yr Roersma 2001; 28% over 2 yr Aldridge 2000), but there were differences in the success of specific breeding life stages. Consider for example that nest success was markedly lower in this system (47%, Chapter 2) compared with that for sharp-tails from the Milk River Ridge in southwestern Alberta (65% over 2 yr, Roersma 2001). Therefore, average values for specific life stages can vary between regions and probably between years. Hence, I present a sensitivity analysis to identify the life stage parameter most important for explaining population density for sharp-tails in this system in a forthcoming paper (Chapter 5).

Brood Habitat Selection

Studies that have examined habitat used by sharp-tail broods have largely focused on microhabitat features ($\leq$ 8-m extent, Moyles 1981, Klott and Lindzey 1990, Saab and Marks 1992, Roersma 2001), rather than at broader scales making direct comparisons difficult. Concealment cover (50-m extent) was an important resource for broods in this study, with selection for greater cover than available at random. Indeed, cover was the strongest variable for explaining selection using ground data in both years, although the model fit was considerably better in 2001 compared with 2000 (Table 3-2). I predicted that broods would select concealment cover in a non-linear relationship by avoiding areas with very sparse and very tall cover. However, this prediction received moderate but inconclusive support from the data in that an inverted U function was better in 2001 but not in 2000. Moreover, concealment cover ratings may have incurred more variability because I did not record brood locations at a specific time of the day. Brood locations were generally taken between sunrise and 4-5 hr after sunrise. Broods in the aspen parkland of Alberta (Moyles 1981) and the pothole region of Saskatchewan (Pepper 1972) used denser habitat during mid-day periods and more open grassland habitats in early morning and later afternoon. Hence, concealment cover may be more important for broods at specific periods of the day than my results demonstrate.

I initially predicted that broods would use mesic areas for food availability and cover (Aldridge and Brigham 2002), but the models did not support this theory. Broods were negatively associated with increasing amounts of wetland habitat at both scales (50 m, 583 m), although the relationships were not particularly strong. Most of the wetland habitat in the study area was void of standing water in 2000 and 2001 except for a very limited number of man-made water catchments. Hence, I conclude that wetland habitat was not strongly avoided nor selected within the study area based on its availability.

There are a number of possible explanations why relatively small portions of deviation (< 4%, Table 3-2) were explained when available habitat was measured at the 1,800-m scale. First, the 6 habitat categories used may have been too coarse and therefore missed more subtle habitat features important for broods. This may have been particularly important at the 50-m scale where GIS data was relatively coarse using 30 X 30-m pixels. Moreover, the small sample of 40 brood locations may have been too small to provide adequate statistical power to detect stronger selection. Had I included all 57 early brood locations in models, statistical power would have improved; however, this approach would have invoked double counting habitat at the scale relevant to selection and thus overstated statistical confidence. On a different track, Aberg et al. (2000) contend it is difficult to detect habitat selection at the scale of the organism, particularly if an area is generally suitable for grouse. The explanatory ability of these models increased as the scale used to define available habitat increased beyond the organism to the regional scale (1,088 km^2), thus supporting the general assertion by Aberg et al. (2000).

Predator Density and Spatial Extent

Northern harriers, red-tailed hawks and Swainson's hawks were the prominent raptors in the study area. Great horned owls were also common but not generally counted in the diurnal census. I do not presume sharp-tails were a major dietary item for raptors, but likely comprised an opportunistic meal where found (Gilmer et al. 1983, Gilmer and Stewart 1984, Houston et al. 1998, Potts 1998). Primary prey for raptors likely included ground squirrels (*Spermophilus* spp.), voles (*Microtus* spp.), deer mice (*Peromyscus maniculatus*) and insects. Raptors, and particularly Swainson's hawk are known to forage on grasshoppers (*Orthoptera* spp.) (England et al. 1997). The abundance of grasshoppers across this region of southern Alberta received national media attention in 2000 and 2001. I casually observed that they were especially abundant in sparse grassland habitat (presumably hatched on bare soils). Hence, it is possible that grasshoppers were an attractive food source drawing raptors into sparse grassland habitats during this study (Fig. 3-1).

The model using sparse grassland to explain raptor density was only 1.3 times better than the next best model. Hence, there was moderate evidence suggesting raptor density was explained by sparse grassland and/or wetland habitat. A positive association between raptors and wetland variables may be linked to a number of factors. Harriers were commonly seen flying low over wetlands void of water, and have been associated with mesic areas in other studies (Potts 1998). Red-tails, Swainson's, and to a lesser degree ferruginous hawks were commonly seen sitting on perch sites. Trees and tall willows were commonly found around wetland edges and hence provided perch and nesting resources commonly used by raptors (Preston 1990, Wolff et al. 1999). Furthermore, wetland areas may hold a variety of prey species that attract raptors as a searching focus point.

Since trees are presumably an important resource for most raptors as nest or perch sites (Preston 1990, Wolff et al. 1999), I was surprised this variable was not among the better models (model s 4, 12, 16, Table 3-3). The lack of pattern between treed habitat and raptor density is not clear, but I speculate there were enough trees across the entire study area to satisfy requirements for nesting. Furthermore, trees were often in stands too small to detect with a GIS, and hence, the grain of resolution was not adequate to quantify whether raptors were associated with trees in the area. On the other hand, broods selected areas with more treed habitat than available at random (50 m), which likely aided avian predators that use perch sites for hunting (Wolff et al. 1999).

Both mammals and raptors kill grouse (Schroeder and Baydack 2001), but the prominence of 1 guild over the other appears to differ between systems, and is probably linked with the suite of resources (habitat and prey) available for each group (Widén 1994, Preston 1990). In forest systems, and in areas where mammalian predators are controlled, raptors can play a prominent role in predation on ground dwelling birds. Raptor kills in forested areas were associated with 78% of the mortalities on ruffed grouse chicks (*Bonasa umbellus*) in Michigan (Larsen et al. 2001), and 40% and 35% of the mortalities on black grouse (*Tetrao tetrix*) and hazel grouse (*Bonasa bonasia*) in Finland (Tornberg 2001). A recent study in southern Scotland suggests red grouse (*Lagopus lagopus*) numbers were limited by raptors (Thirgood et al. 2000). In prairie systems, the majority of predation for galliformes and ducks is commonly attributed to mammalian predators (Klett et al. 1988, Riley et al. 1998). In this study, raptors were associated with 27% of the mortalities for hens and 11% for radio-marked chicks (Chapter 4). Conversely, mammals were credited with a greater portion of the known predator kill events for both hens and chicks (40 and 54% respectively) in this prairie system (Chapter 4).

Brood Success and Habitat

There was moderate support for the hypothesis that brood success was inversely associated with disturbed habitat at broad extents. Hens with less crop and sparse grassland at their home range extent (583 m) were more likely to rear ≥1 chick to 30 days old. This pattern was consistent at 583 and 1,600-m extents, but was 12 times more likely to be better for explaining brood success at the smaller scale. However, the best model explained only 13% of the deviation in brood success suggesting other scales of measure, or important habitat classifications were missed. Raptor density was positively associated with sparse grassland, although this relationship became inverted at higher levels of sparse grassland. Hence, there was indirect evidence linking predator and prey through the association of sparse grassland habitat. However, brood success was not statistically greater in landscapes with lower raptor density. The sample size of broods in landscapes with >0.75 raptors/km^2 was small suggesting the confidence interval used in the estimate may be biased. Therefore, evidence of the pattern between brood success and raptor density was not conclusive, and should be clarified in future work.

Hatch date was not an important variable for explaining whether broods were successful in this study. In contrast, a number of other workers have found positive associations between early hatch dates and survival for ground dwelling broods. Riley et al. (1998) found ring-necked pheasant (*Phasianus colchicus*) chicks in Iowa were less likely to survive if hatched after the median hatch date. A study on Canvasbacks (*Aythya valisineria*) found greater survival associated with ducklings hatched earlier in the season (Anderson et al 2001). Rotella and Ratti (1992) suggested duck broods hatched early in the season had better quality wetland habitat compared with those hatched later. Hence, if the link between hatch date and brood success is a function of habitat resources, then intra and inter-specific competition for resources was probably quite weak in my study.

Studies in Europe have found lower breeding success for grouse (proportion of hens with broods) in relation to land use at landscape scales. Kurki et al. (2000) flushed fewer hens with chicks in landscapes with greater proportions of crop and pastureland, which they related to corresponding increases in the density of foxes (*Vulpes vulpes,* Kurki et al. 1998). In Britain, female black grouse (*Tetrao tetrix*) were more likely to have a brood by mid-summer in lightly grazed landscapes (54%) compared with those in heavily grazed areas (32%, Calladine et al. 2002). Kurki et al. (1995) suggested the pattern between breeding success and agricultural habitat was related to poor nest success rather than differences in brood survival between land use regimes. However, they were unable to verify this assumption because they did not have nest data for individual hens. This work on sharp-tails demonstrates more resolution in the pattern between land use and breeding success. Both brood success and nest success (Chapter 2) were lower in areas with more crop and sparse grassland in this study. Hence, human related habitat disturbance is a problem for sharp-tails in this system and is associated with more than 1 measure of breeding success.

Table 3-1. Explanatory habitat variables for analyzing grouse brood habitat selection (Sel), brood success (BS), and raptor density (Rap) in Alberta. Categorized by habitat surveyed from ground or GIS methods.

Variable	Data type	Description	Analysis
Ground Data			
vor50	continuous	cover height averaged over 100 m transect centered at brood location	Sel
vor50^2	continuous	vor50*vor50 (quadratic term)	Sel
bd50	continuous	bare ground averaged over 100 m transect centered at brood location	Sel
res50	continuous	residual cover averaged over 100 m transect centered at brood location	Sel
shrubL[a]	categorical	shrub density over 100m radius: Low, Med, High.	Sel
perch	categorical	presence of perch site <75m or ≥75m from brood	Sel
GIS Data			
crop50	continuous	log ratio[a] crop: 50 or 583m	Sel, BS
tree50	continuous	log ratio tree: 50 or 583m	Sel, BS
wet50	continuous	log ratio wetland: 50 or 583m	Sel, BS
wat50	continuous	log ratio water: 50 or 583m	Sel, BS
brgr50	continuous	log ratio sparse gd: 50 or 583m	Sel, BS
crop16	continuous	log ratio crop: 1600 or 2265m	Rap
tree16	continuous	log ratio tree: 1600 or 2265m	Rap
wet16	continuous	log ratio wetland: 1600 or 2265m	Rap
wat16	continuous	log ratio water: 1600 or 2265m	Rap
brgr16	continuous	log ratio crop: 1600 or 2265m	Rap
e.crop16[c]	continuous	edge crop: 1600 or 2265m	Rap
e.tree16	continuous	edge tree: 1600 or 2265m	Rap
e.wet16	continuous	edge wet: 1600 or 2265m	Rap
e.dg16	continuous	edge dense grass: 1600 or 2265m	Rap
e.cp16L	categorical	edge of crop: 1600m. Low, Med, High	BS
crop16L	categorical	log ratio crop: 1600m. Low<10%, Med = 10-30%, High = 47-70%.	BS
crbr16L	categorical	log ratio crop+sparse grassland: 1600m. Low = 20-34%, Med = 35-44%, High = 45-70%	BS

[a] Log ratio of (a_i /dense grassland).

[b] Edge density (edge/ha)

Table 3-2. Quasi-likelihood logistic regression explaining selection for sharp-tailed grouse brood sites in Alberta, 1999–2001. Habitat measured from ground surveys are modeled for broods from 2000 (n = 18) and 2001 (n = 24). Habitat measured with GIS data are modeled with broods from 1999–2001 (n = 40). Scale of available habitat in parenthesizes. Evidence for the strongest model (in bold) among those considered was evaluated with Akaike weights (ω_i).

Model	Constant	Explanatory variables		n	k^a	$-2LL^b$	$\Delta AIC_c{}^{cd}$	$\omega_i{}^{de}$	D^f
50-m extent ground data 2000 (1,600m)									
1C^{gh}	-3.16	+0.10 vor50		258	3	125.88	**0.00**	**0.693**	3.6
2C	-3.37	+0.17 vor50	- 0.004 vor50^2	258	4	125.46	1.64	0.305	3.9
3C	-2.42	- 1.15 shrubL	- 0.62 shrubM	259	5	133.23	11.49	0.002	2.0
4C	-2.36	+0.49 perch<75		259	4	140.16	16.35	0.000	1.0
50-m extent ground data 2001 (1,600m)									
5C	-3.82	+0.22 vor50		243	3	120.10	3.17	0.170	25.4
6C^h	-4.86	+0.45 vor50	- 0.01 vor50^2	243	4	114.86	**0.00**	**0.830**	28.7
7C	-2.10	- 1.78 shrubL	- 1.13 shrubM	242	5	152.06	39.28	0.000	5.5
8C	-1.84	+ 1.35 perch<75		242	4	152.66	37.80	0.000	5.1
50-m extent GIS data (1,801m)									
9C	-3.38	- 0.21 wet50	+ 0.24 tree50	1210	4	349.34	2.00	0.181	0.6
10C	-3.47	- 0.11brgr50		1210	3	350.17	0.82	0.326	0.4
11B^g	-3.21	- 0.19 brgr50	+ 0.24 tree50	1210	4	347.34	**0.00**	**0.492**	1.2
583-m extent GIS data (1,801m)									
12C	-0.39	+ 0.28wet583	+ 0.29 tree583	105	4	136.74	3.77	0.132	2.0
13C^h	-0.88	- 0.90 brgr583		105	3	135.13	**0.00**	**0.868**	3.2
583-m extent GIS data (1,088 km^2)									
14C	-0.30	- 0.31 crop583		540	3	271.14	10.62	0.005	4.9
15C	-2.43	- 0.20 wet583	+ 0.40 tree583	540	4	277.65	19.16	0.000	2.6
16C	-2.85	+ 0.45 tree583	- 0.81 brgr583 - 0.37 crop583	540	5	256.45	**0.000**	**0.995**	10.1

[a] k is the number of explanatory variables, plus the constant, plus the variance inflation factor $_c$ (Anderson and Burnham 2002).

[b] The –2log likelihood.

[c] $\Delta_i = AIC_i - minAIC$ (Anderson et al. 2000: 918). Subscript c refers to AIC corrected for small sample bias (Anderson et al. 2000).

[d] ΔAIC_c and ω_i are only comparable among models within the same group (model # 1–4, 5–8, 9–11, 12&13, 14–16).

[e] Estimated probability that model is the best among models considered (Anderson et al. 2000).

[f] Percent deviance explained by model (deviance full model/deviance null model).

[g] C refers to candidate model. B refers to model derived from backward stepwise selection.

[h] Model obtained from backward stepwise selection the same as the candidate model.

Table 3-3. Linear multiple regression explaining the density of raptors related to landscape composition and edge at 2 spatial extents. Estimates were based on counts in 25 landscapes in Alberta in 2000 and 2001. Akaike weights (ω_i) clarify the best model (in bold) within each extent and between extents.

						within extents		between extents	
Model	Constant	Explanatory variables	R^2	k[a]	RSS[b]	ΔAIC_c[c]	ω_i	ΔAIC_c	ω_i
1,600 m									
1	+0.42	+ 0.01 e.wet16	7.0	3	1.25	1.16	0.181	1.16	0.093
2	+0.13	+ 0.002 e.dg16 - 0.01 e.wet16	10.4	4	1.21	3.61	0.053	3.61	0.027
3	+0.44	+ 0.05 brgr16 + 0.01 e.wet16	10.0	4	1.21	3.66	0.052	3.66	0.027
4	+0.49	+ 0.04 tree16 + 0.01 e.wet16	8.1	4	1.24	3.89	0.046	3.89	0.024
5	+0.74	+ 0.07 wet16	6.9	3	1.25	1.16	0.181	1.16	0.093
6[d]	+0.75	+ 0.06 wet16 + 0.04 brgr16	8.6	4	1.23	3.83	0.048	3.83	0.024
7	+0.75	+ 0.004 wat16+ 0.06 wet16	7.0	4	1.25	4.02	0.043	4.02	0.022
8[de]	**+0.59**	**+ 0.12 brgr16 - 0.15 brgr16**^{2}	**35.8**	**4**	**0.87**	**0.00**	**0.323**	**0.00**	**0.166**
9	+0.55	+ brgr16 – brgr16^2 + wet16	36.8	5	0.85	2.98	0.073	2.98	0.037
2,265 m									
10[d]	**+0.38**	**+ 0.01 e.wet22**	**12.0**	**3**	**1.19**	**0.00**	**0.258**	0.56	0.126
11	+0.39	+ 0.05 brgr22 +0.01 e.wet22	13.4	4	1.17	2.68	0.067	3.24	0.033
12	+0.44	+ 0.04 tree22 +0.01 e.wet22	12.7	4	1.18	2.77	0.064	3.33	0.031
13	+0.43	+ 0.001 wat22 +0.01 e.wet22	12.2	4	1.18	2.84	0.062	3.40	0.030
14	+0.82	+ 0.09 wet22	10.6	3	1.21	0.17	0.237	0.73	0.115
15	+0.85	+ 0.10 wet22 +0.03 brgr22	11.2	4	1.20	3.00	0.059	3.52	0.028
16	+0.84	+ 0.10 wet22 +0.0004 tree22	10.7	4	1.20	3.02	0.057	3.58	0.028
17	+0.56	+ 0.18 brgr22 - 0.22 brgr22^2	24.9	4	1.01	1.14	0.146	1.70	0.071
18	+0.46	+ brgr22 + e.wet22 – brgr22^2	31.6	5	0.92	3.28	0.050	3.84	0.024

[a] k is the number of explanatory variables, plus constant, plus variance term (Anderson et al. 2000).

[b] RSS is the residual sum of squares (Anderson et al. 2000).

[c] $\Delta_i = AIC_i - minAIC$ (Anderson et al. 2000: 918). Subscript c refers to AIC corrected for small sample bias (Anderson et al. 2000).

[d] Best model for describing raptor density for each extent based on ω_i.

[e] Best overall model for describing raptor density between extents based on ω_i.

Table 3-4. Quasi-Likelihood logistic regression explaining brood success (n = 40) for sharp-tailed grouse with habitat variables measured at multiple extents, and for hatch date in Alberta, 1999-2001. Evidence for the strongest model (in bold) evaluated with Akaike weights (ω_i) in 3 steps of analysis. Step 1 evaluates the best model within each extent. Step 2 evaluates the best model among extents (1–15). Step 3 evaluates the best overall model (1–18).

								Step 1		Step 2		Step 3	
Model	Constant	Explanatory variables		Extent	D[a]	k[b]	-2LL[d]	ΔAIC_c[e]	ω_i	ΔAIC_c	ω_i	ΔAIC_c	ω_i
1	+0.41	-0.10 wet583		583	0.3	3	51.62	4.05	0.063	4.05	0.055	4.05	0.037
2	+0.02	-0.02 brgr583		583	5.6	3	48.90	1.34	0.244	1.34	0.244	1.34	0.144
3	+0.13	-0.25 crop583		583	3.9	3	49.77	2.20	0.158	2.20	0.139	2.20	0.094
4	+0.75	+0.11 tree583		583	0.1	3	51.73	4.16	0.059	4.16	0.052	4.16	0.035
5B[f]	-0.96	-1.70 brgr583	- 0.38 crop583	583	12.9	4	45.09	**0.00**	**0.476**	**0.00**	**0.417**	**0.00**	**0.281**
6	+0.44	+ 1.01 crop16Low	- 0.15 crop16Med	1600	4.8	5	49.32	1.73	0.110	6.85	0.014	6.85	0.009
7	+0.54	+ 1.07 crbr16Low	+ 0.00 crgr16Med	1600	4.7	5	49.39	1.80	0.106	6.92	0.013	6.92	0.009
8	+0.76	+ 1.74 wet16Low	+ 0.94 wet16Med	1600	8.1	5	47.59	**0.00**	**0.261**	5.12	0.032	5.12	0.022
9	+0.56	+ 0.29 brgr16Low	+ 0.18 brgr16Med	1600	0.2	5	51.71	4.12	0.033	9.25	0.004	9.25	0.003
10	+0.58	- 0.62 tree16Low	- 1.18 tree16Med	1600	4.2	5	49.61	2.02	0.095	7.14	0.012	7.14	0.008
11	+0.58	- 0.62 e.tree16Low	- 1.18 tree16Med	1600	8.1	5	49.61	2.02	0.095	7.14	0.012	7.14	0.008
12	+0.62	+ 0.72 e.crop16Low	+0.27 e.crop16Med	1600	1.7	5	50.94	3.35	0.049	8.47	0.006	8.47	0.004
13	+0.73	+ 1.61 e.wet16Low	+ 0.59 e.wet16Med	1600	6.4	5	48.47	0.88	0.168	6.00	0.021	6.00	0.014
14	+0.54	- 0.12 e.brgr16Low	+ 0.51 e.brgr16Med	1600	1.6	5	50.98	3.39	0.048	8.51	0.006	8.51	0.004
15	+0.58	- 0.29 e.dg16Low	+ 0.00 e.dg16Med		0.3	5	51.65	4.06	0.034	9.18	0.004	9.18	0.003
Best model all extents, GIS and ground													
16	-1.12	- brgr583 -crop583 +wet16L +wet16M		583/1600	18.8	5	44.48					7.74	0.006
17B[f]	-0.98	- 1.70 brgr583	- 0.38 crop583	583	12.9	4	45.09					**0.00**	**0.281**
Hatch date													
18	+0.94	- 0.01 hatchdate			0.6	3	51.49					3.92	0.040

[a] The percent deviance explained by the current model (deviance full model /deviance null model).

[b] k is the number of explanatory variables, plus the constant, plus the variance inflation factor $_c$ (Anderson and Burnham 2002).

[d] The –2log(likelihood).

[e] $\Delta_i = AIC_i - minAIC$ (Anderson et al. 2000: 918). Subscript c refers to AIC corrected for small sample bias (Anderson et al. 2000).

[f] B refers to models derived from backward stepwise selection.

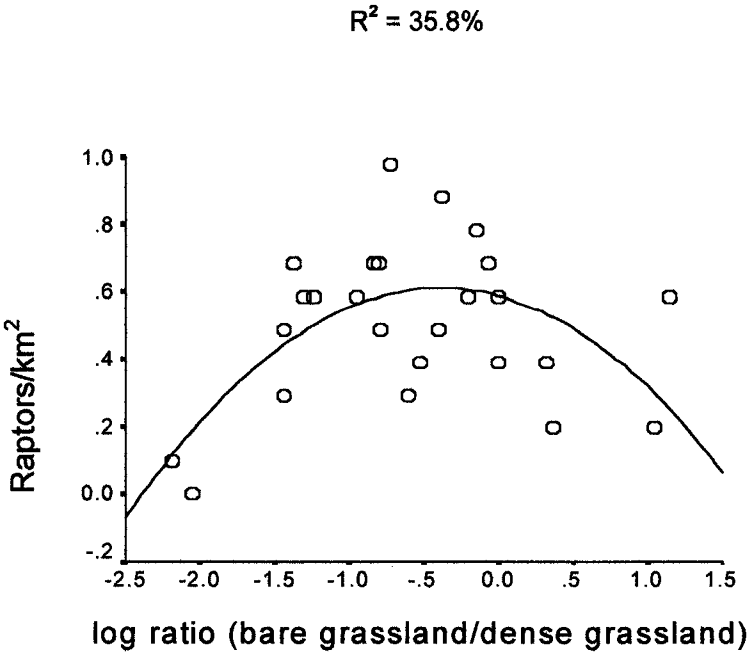

Fig. 3-1. Raptor density in relation to the portion of sparse grassland within a 1,600-m extent. Sparse grassland was quantified as the log ratio of sparse grassland with respect to the amount of dense grassland.

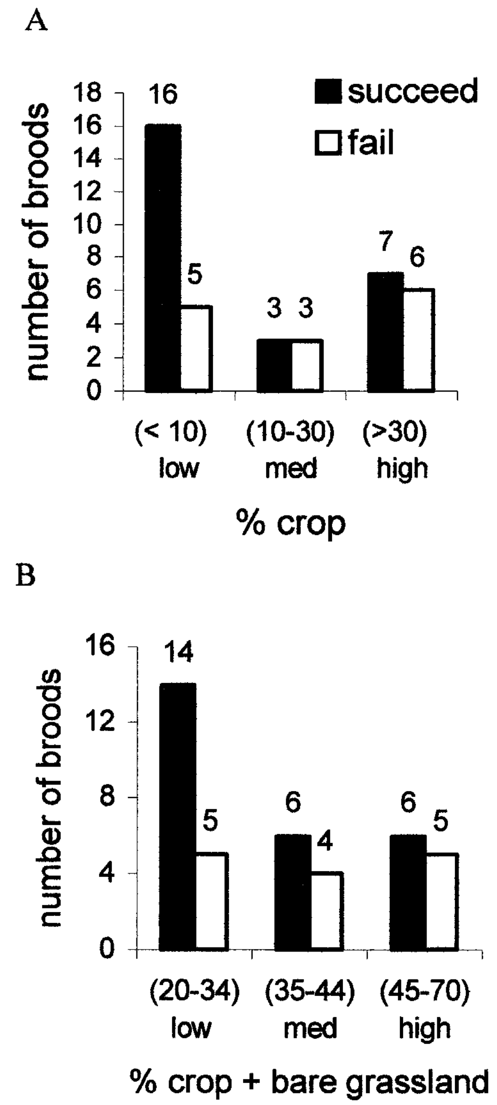

Fig. 3-2. Sharp-tailed grouse broods with ≥ 1 chick alive 30 days post-hatch among landscapes characterized by the proportion of A) crop within a 1,600 m extent , and B) crop and sparse grassland within a 1,600-m extent in Alberta, from 1999 through 2001. Numbers above bars are number of broods.

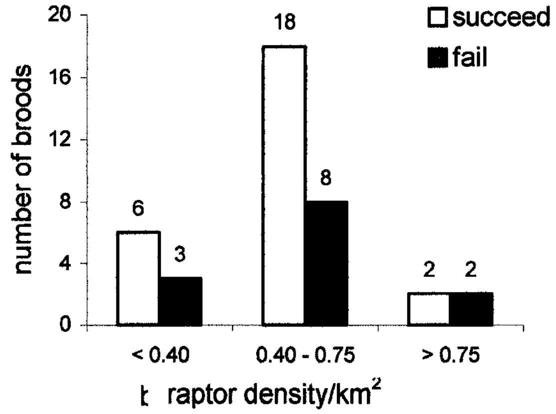

Fig. 3-3. Sharp-tailed grouse brood success in relation to the density of raptors measured at a 1,600-m extent. Numbers above bars indicate number of broods.

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CHAPTER 4

SURVIVAL OF SHARP-TAILED GROUSE CHICKS AND HENS DURING THE BREEDING SEASON

INTRODUCTION

Sharp-tailed grouse (*Tympanuchus phasianellus*, hereafter sharp-tails) have experienced declines in portions of their range over the past century (Connelly et al. 1998). Reasons for these declines are uncertain, however, lower breeding success for ground nesting birds has been associated with increases in cropland (Greenwood et al. 1995) and heavy cattle grazing (Baines 1996, Calladine et al. 2002). Hence, habitat loss or degradation is often stated as the ultimate cause for declines in grassland birds (Schroeder and Robb 1993, Connelly et al. 1998, Giesen 1998, Schroeder et al. 1999), but predation is the proximate cause of mortality for most individuals (Schroeder and Baydack 2001). Indeed predation is an important limiting factor for many bird species (Newton 1993), and increasing predator density has been associated with increasing proportions of crop and pasture land at landscape extents (Andrén 1992, Kurki et al. 1998).

The initial weeks after hatch are a vulnerable time period for grouse (Aldridge and Brigham 2002), but survival rates and factors associated with mortality are not well known (Lindström 1994, Connelly et al. 1998). Predation, along with exposure and food availability, are common explanations of mortality for precocial young (Criddle 1930, Marcström et al. 1988, Johnson and Boyce 1990, Korschgen et al. 1996a, Riley et al. 1998, Park et al. 2001). However, empirical evidence of the causes of mortality for prairie grouse is lacking (Lindström 1994, Connelly et al.

1998, Schroeder et al. 1999) and difficult to obtain because kill events are rarely observed.

The breeding season can be an arduous period for hens as well. Hens invest considerable physical energy in laying and rearing a brood (Erikstad 1986), and can experience heightened predation during this period (Flint and Grand 1997, Hannon et al. in Press). High rates of hen mortality occur over the breeding season for some species of waterfowl (Miller et al. 1995, Flint and Grand 1997), but are not well known for sharp-tails (Lindström 1994, Connelly et al. 1998).

The objectives of this study were threefold. First, to measure survival for sharp-tail chicks from hatch to 30 days old and for hens during the breeding season. Second, determine the probable causes of mortality for chicks and hens. Third, to determine if survival was lower in areas with more human-caused habitat disturbance at landscape extents.

STUDY AREA

The study took place in the Mixed Grass Prairie of southeastern Alberta (51°45'N and 111°W) over an area of 1,392 km^2. Agricultural crops fragmented the grassland matrix across much of the region. Topography was predominately flat with moderate rolling hills towards the southeast. Prominent grasses were fescue (*Festuca* spp.) and needle and thread (*Stipa comata*), and common shrubs included western snowberry (*Symphoricarpos occidentalis*), rose (*Rosa* spp.) and willow (*Salix* spp.). Small patches of aspen (*Populus tremuloides*) were commonly found along north slopes, depressions and around homesteads, but wider encroachment was evident across the matrix. The primary land use was cattle ranching, followed by agricultural crops (wheat, canola, pea). Oil and gas extraction occurred in clusters across the region. Long term precipitation averaged 371 mm per annum in this region (Appendix 2).

Potential avian predators for hens and chicks included birds of prey such as red-tailed hawk (*Buteo jamaicensis*), northern harrier (*Circus cyaneus*), Swainson's hawk (*Buteo swainsoni*), ferruginous hawk (*Buteo regalis*), and great horned owl (*Bubo virginianus*). Corvids in the region included magpie (*Pica pica*) and American crow (*Corvus brachyrhynchos*), which presumably could kill sharp-tail chicks taken from the ground. Coyotes (*Canis latrans*) were abundant, with red fox (*Vulpes vulpes*), skunk (*Mephitis mephitis*), and badger (*Taxidea taxus*) at relatively low densities.

METHODS

Radio Telemetry

Sharp-tails were captured annually in late April from 1999–2001, before nesting, using walk-in funnel traps (Toepfer et al. 1987) at 10–16 leks. Hens were fitted with a 14-g necklace radio collar (Holohil Systems, Carp, Ontario, Canada), and located with a portable receiver and 3-element yagi antenna once every 2–3 days during laying, and once each 5 days during nesting and brood rearing. Radio collars featured a sensor that detected if individuals remained inactive for > 12 hrs, and therefore enabled me to determine whether hens were dead or alive without flushing.

Chicks were fitted with micro-transmitters to estimate survival and determine the probable causes of mortality. I captured all the chicks I could find on hatch-day to 2 days post-hatch, and randomly selected 2 chicks/brood and attached a 1.1-g transmitter (life expectancy 35 days, Holohil Systems, Carp, Ontario, Canada). The transmitter was attached subcutaneously to the skin on the back of the chick using 2 sutures (Burkepile et al. 2002). A sterile needle was inserted through the skin perpendicular to the length of the spine, leaving approximately 3–5 mm between the point of entry and exit. Suture material was fed through the interior of the needle, needle removed, and the suture fed through the holes in the posterior end of the transmitter and tied off. One drop of Krazy Glue™ was placed on each knot and on the bottom side of the transmitter. The transmitter was then placed along the midline of the chick's back. Sutures were secured with the knot and glue allowing a 2–4 mm gap between transmitter and body to allow for growth. Handling took approximately 20–30 minutes per brood, and less than 10 minutes per radio-marked chick. All captured chicks were returned to the hen simultaneously. I did not capture chicks on days with cool temperatures (<12–14 C), nor when precipitation was expected within 1–2 hours. This procedure was approved by the University of Alberta, Animal Care Committee.

During brood rearing, chicks and hens with transmitters were triangulated every 5 days up to 30 days post-hatch to determine if chicks were alive and near the hen. I took readings from approximately 30–50 m to avoid flushing chicks. I approached individual chicks to locate the carcass if the signal was not close to the hen. In the pilot year, I captured radio-marked chicks at each 5 day time interval to inspect the condition of the skin near the transmitter sutures, and to take body measurements. I dropped this approach in 2000 and 2001 to minimize the potentially negative influence of additional handling on survival. At 30 days post-hatch, I attempted to flush all chicks from each brood to estimate survival of chicks. If broods were in very thick vegetation that made it difficult to flush (i.e., clump of willows), I returned the next day to reflush the brood. Radio-marked chicks were recaptured on day 30 with a hand-held net and the transmitter removed by snipping the sutures. I searched for lost hens and chicks with a fixed-wing aircraft intermittently through the breeding season.

Probable Causes of Mortality

Dead chicks and hens were recovered as quickly as possible and categorized by the probable cause of mortality into 6-classes: avian predation, mammalian predation, unknown predation, farm mortality (trampled by cattle, machinery), exposure, and investigator handling. I based predator identification on an overall assessment of the trauma to the transmitter and carcass, and the location of recovery site (i.e. coyote den, fox earth, or raptor nest site). Bite or beak marks on the transmitter, consumed body parts, and pulled vs. chewed feathers were used to assign predator type to either mammal or avian (Korschgen et al. 1996*a*, Riley et al. 1998). If I could not distinguish cause between the 2 predator classes, the death was assigned as unknown predation. Death was classed as exposure if no trauma was found on the carcass or transmitter. Hence, this category may be underestimated if chicks were scavenged post-death, but before I discovered the carcass (Bumann and Stauffer 2002).

Habitat

Habitat composition was estimated with the GIS program Arcview 3.2 (Environmental Systems Research Institute, Inc.) using a Landsat 7 image taken in

1999 at 30 X 30-m resolution. These data were classified using the program PCI Geomatica 8.2 (PCI Geomatics). Aerial photos (1:30,000) and ground truthing were used to improve the accuracy of classification. Accuracy ranged between 80–94.8% for each class with an overall rating of 85.6% (K_{hat}), based on stratified random ground truthing (Jensen 1996).

Habitat across the study area was categorized into 6 classes: dense grassland (39%), sparse grassland (27%), crop (26%), trees (4%), wetland (2%) and water (2%). Dense grassland included areas with perennial grasses and shrub cover. Sparse grassland included areas with perennial grass and shrub, but had more bare ground reflectance than dense grassland. I used ground-surveyed data to calibrate the classification for sparse grassland based on Daubenmire readings with > 25% bare ground. Sparse grasslands were affected by soil type and potentially by heavy live stock grazing over a period of years. Evidence for the relative influence of grazing was anecdotal based on personal communication with landowners and the regional range manager. Crop included cultivated land, hay land, and anthropogenic disturbance (homesteads, country roads). The amount of crop and sparse grassland (<35% vs. ≥35%) was evaluated within a 1,600-m radius of the nearest lek. I categorized habitat in this manner because reproductive success and predator densities were both linked to these categories. Sharp-tail nests were more likely to succeed in landscapes with less than 35% crop and sparse grassland (Chapter 2), and raptor density was associated with landscapes having more sparse grassland at this scale (Chapter 3). For convenience, I refer to landscapes as disturbed or continuous to differentiate between areas with more or less crop and sparse grassland as described above.

Survival

I used the Kaplan-Meier (K-M) function to estimate the survival for radio-marked chicks to 30 days post-hatch (Kaplan and Meier 1958, Pollock et al. 1989). Flint et al. (1995*a*) expanded the K-M approach for cases where survival estimates are desired for more than 1 individual in the same brood. They used a bootstrapping technique that delivers an unbiased estimate of the standard error (SE) to meet the assumption that individuals in the same brood have independent survival. Hence, I used radio-marked chicks as individual sample units but estimated SE by treating broods as clusters to avoid inflating degrees of freedom through pseudoreplication (Flint et al. 1995*a*). Standard error was calculated by re-sampling chicks from broods with replacement using bootstrapping until the number of broods in the original sample was drawn. Standard error was derived from 1,000 runs. The equations explained by Flint et al. (1995*a*: 449) do not explicitly state how to account for right-censored individuals in the K-M estimate (those removed from the sample due to loss or radio-failure). Therefore, I clarify their equations to account for censoring by calculating the number of individuals at risk (r) at each time interval (t) for each brood (i), rather than using the number of chicks per brood at each life stage ($n_{t,i}$). Hence, I subtracted the number of right censored chicks ($c_{t,i}$) from the number of radio-marked chicks per brood to get the number of chicks at risk ($r_{t,i}$) at each life stage such that,

$$r_{t+1,i} = n_{t,i} - c_{t+1,i}$$

I substituted $r_{t,i}$ for $n_{t,i}$ in equations (1), (3) and (5) of Flint et al. (1995*a*: 449) such that the survival ($\hat{S}_{t,i}$) for brood i at time t was

$$\hat{S}_{t,i} = r_{t+1,i} \Big/ r_{t,i} \tag{1}$$

The weighted survival estimate ($\hat{S}_t$) at time t was calculated as

$$\hat{S}_t = \sum_{i=1}^{M_t} r_{t+i,i} \Big/ \sum_{i=1}^{M_t} r_{t,i} \tag{3}$$

and $$SE(\hat{S}_t) = \sqrt{\sum_{i=1}^{M_t} r_{t,i}^2 \, (\hat{S}_{t,i} - \hat{S}_t)^2 \Big/ M_t \bar{r}_t^2 (M_t - 1)} \tag{5}$$

where $$\bar{r}_t = \sum_{i=1}^{M_t} r_t \Big/ M_t$$

and M_t refers to the number of marked hens at time t. The K-M function was then used to estimate survival for the period of interest

$$\hat{S}(\mathrm{t}) = \prod_{j=1}^{t} \hat{S}_j \tag{6}$$

I estimated hen survival using the K-M function (Pollock et al. 1989). Survival over the breeding season was measured from 1 May to 13 Aug annually based on a 5-day interval. If hens survived more than 1 breeding season, I randomly selected 1 year for that hen to include in the breeding season survival estimates. Individuals were right censored if their signal could not be located due to loss or failure. Winter survival was not the focus of this study nor did I monitor hens during the winter months. However, I searched for hens in April of the following year and used the return count as the measure of survival. Hence, over-winter survival was based on those at risk from Aug 14 (t_0) to April 30 of the following year ($t+1$) using the K-M function. I used the estimate of over-winter survival to assist in calculating the portion of annual mortality that occurs during the breeding season.

To determine whether the transmitters increased the mortality of chicks, I compared survival to 30 days for non-radio-marked chicks estimated from flush counts with that for radio-marked chicks. All broods received similar handling so marked vs. non-marked chicks differed only in the physical attachment and wearing of the transmitter. Flush counts were done on foot by investigators searching systematically in a grid pattern over a 100-m radius of the suspected brood location. I calculated the K-M estimate of survival for non-radio-marked chicks using the number of chicks hatched at time zero (N_{t0}), less the number of radio-marked chicks, and compared this figure to the number of chicks from all broods flushed at 30 days post hatch (N_{t+1}), (less radio-marked chicks). The total number of chicks hatched was derived by summing the number of eggs hatched per clutch for all the broods in the sample.

Survival rates were compared between habitats, years, and marked vs. non-marked chicks using the Chi-square methods described by Sauer and Williams (1989). Alpha levels were set to 0.10 to guard against type II errors. Means are reported with standard errors. Analyses were modeled in Microsoft Excel with the Pop Tools extension (version 2.2).

RESULTS

Chick Survival and Mortality

Survival was 0.41 ± 0.08 (95% CI 25–57%) to 30 days post-hatch. Most of the mortality (73%) occurred during the initial 15 days (Fig. 4-1). Survival was statistically similar among years (1999 = 0.18 ± 0.15, n = 11; 2000 = 0.40 ± 0.18, n = 29; 2001 = 0.53 ± 0.12, n = 30; $\chi^2 = 3.42$, 2 df, $P = 0.18$), and between continuous and disturbed landscapes (0.42 ± 0.15, n = 46, and 0.38 ± 0.13, n = 24 respectively, $\chi^2 < 0.01$, 1 df, $P > 0.95$). Seasonal rainfall was greater than average in 1999, and lower than average in 2000 and 2001 (Appendix 2 Fig. A-2-1).

Predation accounted for most (68%) chick deaths, followed by exposure, farm activity, and investigator related mortality after handling (Table 4-1). Mammals killed more chicks than avian predators. Three broods had >1 radio-marked chick killed during the same 5-day interval; chicks from 2 of these broods were killed by predators (3 from mammals and 1 unidentified predator) and those in the third brood were trampled by cattle.

I performed survival analysis on 70 chicks from 35 broods, excluding 2 chicks that probably died because of handling. Survival for 303 (n = 34 broods) non-radio-marked chicks to 30 days post-hatch was lower (0.25 ± 0.003) than that for radio-marked chicks (0.41 ± 0.08, $\chi^2 = 24.03$, 1 df, $P < 0.01$).

Hen Survival and Mortality

I monitored 111 hens over 3-years with an overall survival of 0.53 ± 0.05 (95% CI 44–63%) during the breeding season (Fig. 4-2). Survival was not different among years (1999 = 0.58 + 0.10, n = 26; 2000 = 0.52 ± 0.09, n = 38; 2001 = 0.53 ±

0.08, n = 47; $\chi^2 < 0.01$, 2 df, $P > 0.95$). Predation accounted for 96% of hen mortalities. Mammals were responsible for more deaths than raptors, but 31% of predator kills could not be assigned to a specific predator type (Table 4-1). Over-winter survival was 0.81 ± 0.01 (95% CI 79–82%, n = 52), over 3-years. Survival was moderately lower for hens in disturbed landscapes (0.45 ± 0.07, n = 65), compared with those in continuous habitat (0.62 ± 0.07, n = 46; $\chi^2 = 3.00$, 1 df, $P = 0.09$; Fig. 4-3).

DISCUSSION

Chick Survival and Mortality

Early survival and causes of mortality are not well known for prairie grouse chicks. My estimate of 41% survival for 30 days post-hatch is similar to ring-necked pheasant chicks (*Phasianus colchicus*) in Iowa (Riley et al. 1998), which averaged 46% and 37% in 2 study areas over 4-years. Survival for ruffed grouse (*Bonasa umbellus*) chicks for ≥ 80 days over the brood rearing season was 29 and 32% over 2-years; however, transmitters were not fit on chicks until 5–10 days old, which probably underestimated early mortality (Larson et al. 2001). Sharp-tail chicks were particularly vulnerable in the early stage of brood rearing with the majority of deaths occurring by the time chicks were 15 days old (Fig. 4-1). High early mortality is common for ground dwelling precocial young including waterfowl (Flint et al. 1995*b*, Korschgen et al. 1996*a*) and galliformes (Zwickel and Bendell 1967, Riley et al. 1998).

Similar to other studies on precocial young in prairie systems, predation accounted for the majority of deaths with mammals taking more than avian predators

(Table 4-1). Mammals accounted for the majority of predation for ducklings < 4 weeks old in a prairie/forest ecotone (54%, Korschgen et al. 1996*a*), and for ring-necked pheasant (hereafter pheasant) chicks in a prairie biome (85%, Riley et al. 1998). In contrast, 78% of the predator kills on ruffed grouse chicks in a forest matrix were from avian predators (Larson et al. 2001). Avian kills accounted for 27% of the identified hen mortalities in this study compared with only 11% for chicks. I may have underestimated avian kills in the chick analysis because evidence was less distinctive than for mammals. Mammals appeared to pull off the transmitter by gripping the antenna with their teeth, which often left distinct marks. Avian predators presumably applied a similar approach by ripping off the transmitter, but beak marks were less obvious. Evidence used to assign an avian kill included such things as fecal spray at the location site, transmitter in or below nest, pulled feathers and unconsumed grouse entrails. I was unable to distinguish between mammalian and avian kills for 8 chicks. If the majority (5 of 8) were from avian predators, then the portion of avian kills on chicks (9/38 = 24%) would be similar to that for hens.

Exposure accounted for 13% of chick mortalities, which is slightly greater than the 7% associated with pheasant chicks in Iowa (Riley et al. 1998), or the 11% for ducklings in Minnesota (Korschgen et al. 1996*a*). Death from exposure appears to be associated with periods of heavy precipitation (Korschgen et al. 1996*a*, Riley et al. 1998). For example, I found a dead hen with 6 chicks underneath (not radio-marked) following 3 days of heavy rain in 1999. The carcasses were intact but sodden after the precipitation. Roersma (2001) reported a similar case of a hen and brood found dead, presumably from exposure, after severe weather in 1998.

Exposure probably accounts for some chick losses in many years, but the evidence to date suggests that the overall proportion of mortality from exposure is relatively low in most years. However, heavy losses in a single year presumably could occur if a prolonged period of wet and cold weather persisted through the early stages of chick growth before chicks are able to thermoregulate themselves. Bousquet and Rotella (1998) suggest poor weather was likely responsible for a year of very low sharp-tail chick survival in Montana in 1995.

Determining the cause-specific mortality of marked chicks or hens has subjective bias that is difficult to eliminate (Bumann and Stauffer 2002). Chicks killed from exposure were presumably available for scavenging before recovery, and hence I may have underestimated exposure kills. Moreover, secondary predation events can obscure evidence between predator types (Bumann and Stauffer 2002). For example, if a second predator scavenged or stole a carcass from the initial predator, I could have misclassified the kill in favor of the scavenging predator. I attempted to guard against bias in predator identification by recording kills as "unknown predator" if kill evidence was contradictory or insufficient. Hence, I had many unknown predator kills for both chicks and hens. Notwithstanding these efforts, bias may have occurred in my categorization of kill events and therefore I present these data as probable causes of mortality rather than definitive statements.

The effect of transmitters on survival has been studied in captive populations of ducklings (Korschgen et al. 1996*b*, Davis et al. 1999) and pheasant chicks (Ewing et al. 1994), with neither study reporting a significant difference in survival between young with or without transmitters. My method of fitting transmitters with sutures

(Burkepile et al. 2002) was presumably less intrusive that the subcutaneous implant of transmitters in the pheasant study. Transmitters ranged from 6 to 8% of body weight when initially attached in this study, compared with 7% for pheasant chicks (Ewing et al. 1994).

In calculating survival, I assumed that the transmitter for chicks and hens did not affect mortality. In reality, I expect the process of capture, telemetry and wearing a transmitter probably does have a moderate influence on mortality. However, I found that survival of non-marked chicks was lower than for radio-marked chicks. I attribute this to an underestimation of brood size during flush counts due to chicks that did not flush. Comparing survival between marked and non-marked chicks emphasizes the bias associated with estimating survival on flush counts alone. Flush counts are inherently biased low since some individuals may not flush. This is particularly relevant in areas with dense escape/concealment cover or before chicks develop strong flight (< 15 days post-hatch).

Chick survival appeared low in 1999 compared with other years, although not statistically different. I believe the survival estimate in 1999 was biased low when considered on its own because of a low sample size ($n = 11$) and unusual mortalities that occurred in that year. Because 1999 was the first year using the transmitter technique on chicks, I limited the sample to 11 chicks from 4 broods. Three radio-marked chicks from the same brood were trampled by cattle in 1999, which appears to be an anomaly compared with the sample of chicks in 2000 and 2001 (Table 4-1). Additional handling in 1999 may also have contributed to lower survival.

Hen Survival and Mortality

The breeding period can be a vulnerable time for ground dwelling females attending to nests and broods (Flint and Grand 1997). Sharp-tail hen survival was lower over the breeding season than the rest of the year with ≈ 82% of annual mortality occurring from 1 May to 13 Aug. Survival over the breeding season (53%) was similar to greater prairie-chicken (*T. cupido*) hens in Minnesota (57%, Svedarsky 1988), greater than Attwater's prairie-chicken (*T. cupido*) in Texas (36%, Lutz et al. 1994), but considerably lower than that reported for sharp-tail hens from the Milk River Ridge of Alberta (≥75%, Roersma 2001). The Milk River Ridge study used the same radio transmitter and similar telemetry techniques as this study, suggesting that real differences in survival rates occurred between the 2 regions. Survival may vary markedly between years in some systems (Perkins et al. 1997), but this does not appear to account for differences in 1999 between these 2 regions. In 1999, breeding season survival was greater (78%, n = 18) on the Milk River Ridge compared with hens in this study area (56%, n = 26).

Seasonal estimates of survival are generally not well known for sharp-tails (Lindström 1994). Annual survival estimates are usually near or below 55% for greater prairie-chicken (Schroeder and Robb 1993), lesser prairie-chicken (*T. pallidicinctus*) (Giesen 1998) and sharp-tails (Connelly et al. 1998). I did not monitor hens actively over winter so my measurement for this period was coarse, however, hen winter survival (n = 52, 81%) was greater than for male sharp-tails (<43%) in a portion of Alberta parkland over different years (Moyles and Boag 1981). Mortality for hens during the breeding season is probably linked with high levels of parental investment (Hannon et al. In press), including periodic travel to and from the nest during laying and incubation, increased movement and calling while rearing broods, as well as the risk associated with distracting predators away from chicks.

High proportions of mortality from predation are common for gallinaceous birds outside a hunting season (Keith and Rusch 1989, Schroeder and Baydack 2001, Riley and Schultz 2001). Mammals are prominent predators in many systems and accounted for the majority of hen kills in this study followed by raptors. Svedarsky (1988) found a similar portion of mammalian vs. avian kills on hen prairie-chickens in Minnesota. A study in Iowa looked at pheasant survival over 5-years and found that mammals accounted for 68% of hen mortalities (Perkins et al. 1997). Mammals accounted for a similar portion of known mortalities for hens and chicks in this study (39 and 37% respectively). In contrast, raptors play a prominent role in the predation of grouse in other systems. For example, Goshawks (*Accipiter gentilis*) were responsible for the majority of deaths for black grouse (*Tetrao tetrix*) hens in a forest matrix in Sweden (Angelstam 1984). In northern Finland, grouse are the main diet of goshawks and accounted for 40% of the annual mortalities for black grouse and 35% for hazel grouse (*Bonasa bonasia*) (Tornberg 2001). Harriers also play a major role in the predation of red grouse (*Lagopus lagopus*) in Scotland where mammalian predators are actively managed (Redpath 1991).

Survival and habitat

Survival was moderately greater for hens in landscapes with <35% crop and sparse grassland compared with those in areas with ≥ 35% (Fig. 4-3). Patterns between measures of breeding success and habitat measured at landscape extents have been demonstrated (Andrén 1992, Kurki et al. 2000), but there is less evidence for associating survival with habitat (Riley et al. 1998). One possible explanation for lower survival in more altered landscapes is an increase in the density of generalist mammalian predators as the proportion of agriculture increases within the landscap (Kurki et al. 1998). Hen survival over the breeding season appears to be lower in my study area compared with that on the Milk River Ridge (Roersma 2001), which suggests that the efficiency, density or community of predators is different between the 2 areas. The Milk River Ridge is a nearly continuous landscape of grassland habitat in contrast to the more disturbed landscape in my study area. Manzer (Chapter 3) demonstrated that raptor density was greater in landscapes with more sparse grassland within the study area (non-linear), which may partially explain lower hen survival in areas with more sparse grassland in this analysis. I did not measure mammalian predator density, but speculate that coyote densities may increase with landscape scale habitat disturbance similar to that described for fox densities in Finland (Kurki et al. 1998). Since mammals were responsible for the majority of identified chick and hens kills, clarifying the relationship between mammalian predator density and landscape would be a valuable next step for understanding the risks associated with habitat change.

Lower avian breeding success has been associated with human-related habitat alterations measured over broad extents (Kurki et al. 2000), so I predicted chick survival would be lower in more disturbed areas. For example, duck nesting success was inversely related to the amount of crop at landscape extents in the prairie pothole region of Canada (Greenwood et al. 1995). Black grouse (*Tetrao tetrix*) had fewer hens with broods (Calladine et al. 2002) and fewer chicks per brood (Baines 1996) in more heavily grazed areas in England. Moreover, Manzer (Chapter 2 and 3) found lower nest success and brood success ($\geq$ 1 chick alive to 30 days post-hatch) in areas with more crop and sparse grassland measured at broad extents (1,600 m and 583 m respectively). However, sharp-tail chick survival was not statistically different between disturbed and continuous habitat measured at the 1,600-m extent in this analysis. Nor did a similar study on radio-marked pheasant chicks find a difference in survival between landscapes categorized by the proportion of grassland (Riley et al. 1998). Hence, the risk of predation was greater for hens in altered landscapes at the 1,600-m scale, but the evidence for individually marked chicks is lacking.

Determining a statistical difference in the survival for chicks between habitat classes (or years) was unlikely based on the relatively large standard error. However, notwithstanding the lack of statistical power, mean survival between the 2 landscape types was similar (38% vs. 42%) suggesting chicks were similar in vulnerability in both landscapes at the 1,600-m extent. Sharp-tail brood success was negatively related to crop and sparse grassland at the 583-m scale (Chapter 3), but this relationship explained only a moderate proportion of the variation in success (13%). Hence, the habitat characteristics most important for explaining chick survival may be at a much smaller scale than I measured. Nest success was best explained by habitat models that included concealment cover at the 50-m extent (Chapter 2). This smaller scale and variable may also be important for chicks, but is very difficult to account for given its dynamic nature over space and time for precocial young.

Management Implications and Future Work

Documenting survival for chicks and hens is an important step toward understanding population trends for sharp-tails. There are no individual estimates of early chick survival for sharp-tails, nor prairie grouse in general, so these data are an important contribution towards clarifying this parameter. Flush counts are a common approach for estimating early chick survival for gallinaceous birds, and can be applied with less effort, expense, and expertise than taking my approach with micro-transmitters. I encourage the use of flush counts for this process, but recommend they be considered as minimum estimates that are probably underestimated. I suggest that flush counts be calibrated with survival estimates derived from radio-marked chicks to more accurately approximate this life stage. This may be applicable for workers using these data in a population growth assessment parameterized from specific vital rates for reproduction and survival. For chick survival in this study area, flush count estimates could be scaled up by a factor of ≈1.64 (range 1.00 to 2.28, 0.25/0.25 and 0.57/0.25) to approximate radio-marked chick survival estimates.

Hens in this population experienced high mortality over the breeding season compared with another population in Alberta suggesting considerable variation between locations, or possibly years. I will model the sensitivity of annual sharp-tailed grouse density to the life stage parameters in an upcoming paper to pinpoint the most vulnerable life stage affecting long-term population trends for sharp-tails. Due to the variation in hen survival between regions in Alberta, I anticipate considerable variation can occur between regions for other life stage parameters as well. Accounting for the variation within demographic parameters can affect the rank of elasticities and therefore management alternatives (Wisdom et al. 2000). Chick survival was identified as the life stage with the most influence on the population response for greater prairie-chicken (Wisdom and Mills 1997), so the demographic data from this study will provide a relevant comparison between 2 prairie grouse species.

Table 4-1. Probable causes of mortality for radio-marked chicks and hens during the breeding season for sharp-tailed grouse in Alberta from 1999–2001.

	Chicks	%[a]	Hen	%[a]
Mammal	14	37	19	39
Avian	4	11	13	27
Exposure	5	13	1	2
Cattle/machine	5	13	1	2
Unknown predator[b]	8	21	15	31
Investigator	2	5		

[a] Proportion of mortalities.

[b] Predator kill, but not enough evidence to distinguish as mammal or avian.

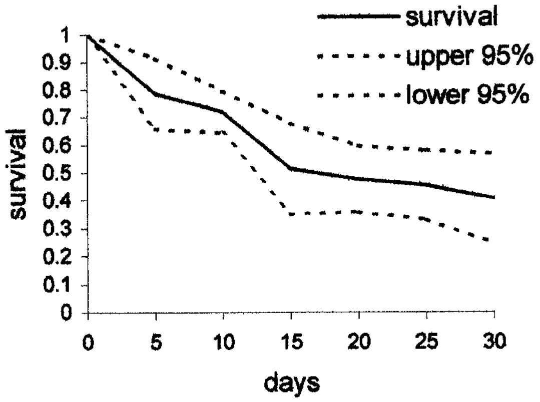

Fig. 4-1. Kaplan-Meier survival function for 70 radio-marked sharp-tailed grouse chicks from 35 broods in Alberta, 1999–2001.

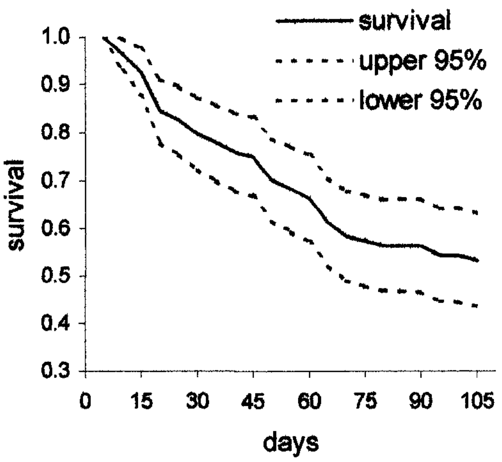

Fig. 4-2. Kaplan-Meier survival function for 111 sharp-tailed grouse hens during the breeding season in Alberta from 1999–2001.

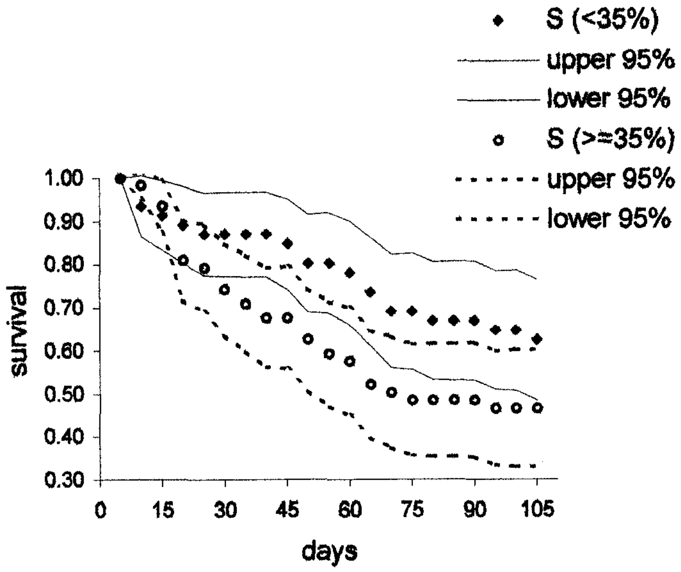

Fig. 4-3. Kaplan-Meier survival functions (S) for 111 sharp-tailed grouse hens during the breeding season over 3-years in landscapes differentiated by the amount of crop and sparse grassland (< 35% vs. ≥ 35%) within a 1,600-m extent.

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CHAPTER 5

SIMULATING MANAGEMENT ALTERNATIVES FOR SHARP-TAILED GROUSE IN HUMAN DISTURBED LANDSCAPES

INTRODUCTION

The rate of growth for a population can differ spatially, with some landscapes producing a net surplus of recruits while others a net deficit. Pulliam (1988) described how sub-populations could function in a source/sink dynamic facilitated by immigration and emigration between landscapes. Identifying habitat associated with a source/sink dynamic is particularly important for characterizing and prioritizing management areas for species of concern (Perkins et al 2003).

Breeding success for grouse and waterfowl is often lower in landscapes fragmented by crop and pastureland than in more pristine landscapes (Klett et al. 1988, Greenwood et al. 1995, Baines 1996, Kurki et al. 2000, Calladine et al. 2002, Chapter 2). Disturbed landscapes often have high densities of generalist predators that prey on nests of ground-nesting birds (Andrén 1992, Kurki et al. 1998, Chapter 2). Moreover, the searching efficiency of predators can improve in areas of smaller patch size, areas with low concealment cover for nests, or where perch sites are available (Paton 1994, Pasitschniak-Arts et al. 1998, Calladine et al. 2002, Chapter 2). Hence, prey in areas with habitat disturbed at small and broad scales may incur greater predation that leads to lower population growth.

Sharp-tailed grouse (*Tympanuchus phasianellus*, hereafter sharp-tails) are 1 of 4 species of grouse that commonly occupy grassland habitats in North America. Grasslands have undergone wide-scale human-caused disturbance since European settlement. Hence, this group of prairie grouse has suffered declines in range and number from historic levels (Schroeder and Robb 1993, Giesen 1998, Connelly et al. 1998). I conducted an intensive demographic study on sharp-tails, and evaluated reproduction and survival in 2 landscape types that differed in the amount of crop and sparsely covered grasslands (sparse grassland) at scales relevant to grouse and potential predators. My intention was first to assess if λ was lower in areas with more disturbed landscape. Second, to determine the amount and combination of changes to particular vital rates necessary to bring $\lambda \geq 1$ in disturbed landscapes.

My specific objectives involved 3 progressive steps. First, I examined the rate of population growth in human disturbed and continuous landscapes by estimating the number of times λ was ≥ 1 based on 1,000 replicates of a stochastic matrix model. I also estimated the elasticity of λ to specific vital rates in these 2 landscape types. Second, I took a retrospective snapshot of the contribution vital rates had on λ. I predicted λ would be particularly sensitive to reproductive vital rates (Wisdom and Mills 1997, Wisdom et al. 2000). Third, I used a prospective simulation analysis to evaluate hypothetical management alternatives that targeted a change in population growth in human disturbed landscapes ($\lambda \geq 1$ in 50% of runs). The first scenario used a reduction in hunting kills to decrease the annual mortality of hens and juveniles. The second scenario assumed that managing habitat for more concealment cover near the nest would positively influence a) nest success and b) hen survival over the breeding season. Scenario 3 combined the effects of restricting fall hunter kills and managing habitat for greater concealment cover over the nesting season.

STUDY AREA

The study occurred in the Mixed Grass Prairie of southeastern Alberta (51°45'N and 111°W) over an area of 1,392 km^2. The matrix was predominately grassland, but with considerable fragmentation by agricultural crops. I chose to work in this area because it encompassed a gradient in the amount of grassland fragmented by crop. Topography was predominately flat with moderate rolling hills towards the southeast. Prominent grasses were fescue (*Festuca* spp.) and needle and thread (*Stipa comata*), and common shrubs included western snowberry (*Symphoricarpos occidentalis*), rose (*Rosa* spp.) and willow (*Salix* spp.). Trees were scattered across the study area in pockets of aspen (*Populus tremuloides*) found in depressions, along north slopes and around homesteads, but wider encroachment was evident across the landscape. Ranching was the predominate landuse, followed by agricultural crops (wheat, canola, pea). Oil and gas extraction occurred in clusters across the region. Long term precipitation averaged 371 mm per annum in this region (Appendix 2).

METHODS

Habitat

I used a GIS to quantify habitat composition using a Landsat 7 image taken in 1999 at 30 X 30-m resolution (Arcview 3.2, Environmental Systems Research Institute, Inc.). I classified these data using the program PCI Geomatica 8.2, and used aerial photos (1:30,000) and ground truthing to improve the accuracy. Accuracy ranged between 80-94.8% for each class with an overall rating of 85.6% (K_{hat}), based on stratified random ground truthing (Jensen 1996). Habitat was categorized into 6 classes: dense grassland (39%), sparse grassland (27%), crop (26%), trees (4%), wetland (2%) and water (2%, Table A-3-1). Dense grassland included areas with perennial grasses and shrub cover. Sparse grassland included areas with perennial grasses and shrubs, but had more bare ground reflectance than dense grassland. I used ground-surveyed data to calibrate the classification for sparse grassland based on Daubenmire readings with more than 25% bare ground. Soil type and heavy stock grazing presumably influenced whether grasslands were identified as dense or sparse. Evidence for the relative influence of grazing was anecdotal based on personal communication with landowners and the regional range manager. Crop included cultivated land, hay land, and anthropogenic disturbance (homesteads, country roads).

I assessed sub-populations of sharp-tails within landscapes categorized by the amount of crop and sparse grassland (aggregated, <35% *vs.* ≥35%) within a 1,600-m radius of the nearest lek (8 km^2). This area loosely describes the breeding complex around leks used by most hens for nesting and rearing a brood (Chapters 2 and 3). It is also the extent that best explains the density of 2 prominent predator guilds in this system (corvids and raptors, Chapters 2 and 3). Further, nests were more successful (Chapter 2) and hens more likely to survive the breeding season in landscapes with less than 35% crop and sparse grassland (Chapter 4), compared with those in ≥ 35%. For convenience, I describe these 2 landscape types as continuous (landscape C, < 35%) and disturbed (landscape D, ≥ 35%).

Field Methods

Sharp-tails were captured annually in late April from 1999–2001, prior to nesting, using walk-in funnel traps (Toepfer et al. 1987) at 10–16 leks. Hens were fitted with a 14-g necklace radio collar (Holohil Systems, Carp, Ontario, Canada), and located with a portable receiver and 3-element yagi antenna once every 2–3 days during laying, once each 5 days during incubation, and daily within 1–3 days of hatch. To avoid causing abandonment or alerting predators to a nest site, I only visited nests to determine clutch size, number hatched, or nest depredation if the hen was not present. Radio collars featured a movement sensor that detected if individuals remained inactive for > 12 hrs, and therefore enabled me to determine if hens were dead or alive without flushing.

I fit micro-transmitters to chicks to determine probable causes of mortality and to estimate survival from hatch to 30 days post-hatch (Chapter 4). I captured all the chicks I could find on the day of hatch up to day 3, and randomly selected 2 chicks/brood and attached a 1.1-g transmitter (life expectancy 35 days, Holohil Systems, Carp, Ontario, Canada). The transmitter was attached subcutaneously to the skin on the back of the chick using 2 sutures (Burkepile et al. 2002, Chapter 4).

During brood rearing, chicks and hens with transmitters were triangulated every 5 days to 30 days post-hatch to determine if chicks were alive and near the hen. I took readings from approximately 30–50 m to avoid flushing chicks. I approached individual chicks to locate the carcass if the signal was not close to the hen. At 30 days post-hatch, I attempted to flush all chicks for each brood to gain an estimate of survival per brood. I continued to locate hens with and without broods until mid-late August annually. I searched for lost hens and chicks with a fixed-wing aircraft intermittently through the breeding season.

Vital Rates

Clutch size (CLUTCH) was derived from counting the number of eggshells following a successful hatch, or within 5 days of depredation for failed nests. Some nests were located late in the laying stage and egg counts were used to verify clutch size at hatch or depredation. Estimates may be biased low if partial clutch loss occurred during laying or incubation. I did not include nests where it appeared that eggshells were removed from the nest area, or were scattered over a wide area around the nest site. Hence, the majority of samples in CLUTCH estimates were from nests that were successful. Eggs were laid on the ground in a shallow depression. Mean parameter values of vital rates and their respective 95% confidence interval (CI) are summarized in Table 5-1.

Hatch rate (HATCH) was based on the number of chicks hatched as a proportion of the number of eggs laid in successful nests. HATCH may be biased high if partial clutch loss occurred and eggs were removed. I assumed a constant sex ratio (SEX) of 1:1.

Nest were considered successful if ≥ 1 egg hatched. Nest success (NEST) was estimated from the number of nests that succeeded / the number that were initiated. I did not use a Mayfield estimate because most nests were found during late laying or early incubation. To avoid pseudoreplication, I limited the sample of nests to 1 per hen regardless of whether an individual nested more than once in a season or nested in more than 1 season. Hence, I combined success for first nests and re-nests into 1 estimate. I believe nest success rates were not biased low due to investigator disturbance because field workers used extreme caution near nests. I avoided flushing hens from nests, nor were nests flagged or overtly marked.

Chick survival (CHICK) from hatch to day 30 was based on Kaplan-Meier (K-M) survival estimates of radio-marked individuals (Chapter 4). Standard errors (SE) and the resulting 95% CI were based on a re-sampling bootstrap technique that treated chicks as sample units but broods as clusters (Flint et al. 1995, chapter 4 this study). This bootstrapping approach was used to avoid overstating the degrees of freedom and hence understating the SE used for constructing the 95% CI.

Survival of juveniles from 31 days post-hatch to the following spring (JUV) was estimated from radio-marked juveniles in a lesser prairie-chicken (*T. pallidicinctus*) population in Kansas (Pitman 2003, Hagen 2003). I did not radio-mark juvenile sharp-tails in the study population and therefore base this vital rate on the best known data available from lesser prairie-chicken in a prairie system. Hagen (2003) estimated juvenile survival of prairie-chicken from 34 days post-hatch to the following March 31 to be 0.54 ± 0.09 (SE, 95% CI 37–71%, n = 32).

Survival of hens over the breeding season (HENBREED) was based on K-M survival estimates for radio-marked hens from 1 May to 13 Aug (Chapter 4). Survival for hens over the winter (HENWINTER) was derived from K-M estimates of radio-marked individuals from 14 Aug to 30 April (Chapter 4). To avoid pseudoreplication, survival was estimated using 1 breeding season and 1 over-winter period per hen (at random) regardless of how many years an individual lived. I did not monitor hens over winter, so over-winter survival was derived from the number of females alive as of 14 Aug (t_0), and those determined alive, dead or censored at April 30 of the following year (t+1).

Stochastic Matrix Population Model

I used a female-based, age-structured, stochastic matrix population model to estimate λ, and the elasticity of λ to matrix elements and lower-level vital rates (Beissinger and Westphal 1998, Caswell 2001). I assumed yearling and adult hens had the same reproductive contribution, hence age at initial breeding was set at 1 year. The probability of breeding was set at 1 because all hens attempted to nest, or were killed before or during nesting. The expected number of female chicks surviving to year t+1 was estimated as $F_i * P_0$, where

$$F_i = (\text{CLUTCH*HATCH})\text{*NEST*SEX}$$

and

$$P_0 = \text{CHICK*JUV}$$

Survival of yearling (P_1) and adult hens (P_2) was derived by

$$P_i = \text{HENBREED*HENWINTER}$$

Reproductive output was summed from the contribution by yearling and adult hens ($Fi*P_0$) in a pre-breeding matrix model (Beissinger and Westphal 1998). All statistical analyses were done using Excel spreadsheets. Means are reported with SE or CI.

Population growth is the change in population size (N) from time t (N_t) to t+1 (N_{t+1}) and is calculated arithmetically by $N_{t+1} / N_t = \lambda$ (Gotelli 1995). The stable-age distribution (w, Caswell 2001), and λ were derived using an Excel spreadsheet. I applied 3 main steps to run the stochastic matrix model: 1) random values were selected for each vital rate within the respective variance range for each replicate of the model; 2) 1,000 resampled replicates of the model were drawn such that each replicate represented a random configuration of vital rate values; and 3) λ and the observed 95% CI were derived from the bootstrapped distribution of the 1,000 replicates (eqn. 12.18, Caswell 2001). The mean and variance for each vital rate were derived primarily from 3 years of data, hence I was hesitant to assume a particular distribution (i.e. normal) given the limited number of years to account for variability (Boyce 1992, Beissinger and Westphal 1998). Therefore, I took a conservative approach and applied a uniform distribution over the range of values within a 95% CI when resampling vital rate values for each replicate. Numbers in the model were truncated to real integers to avoid overstating λ. I report the number of times λ was ≥ 1 out of the 1,000 replicates as a measure of population viability in a probability context (Wisdom et al. 2000).

The rate of change in a population is a function of survival, reproduction, immigration and emigration. For modeling purposes I assume the population is closed and therefore do not account for individuals leaving or entering landscapes. The relationship between λ and survival and reproductive parameters is commonly described in terms of sensitivity and elasticity. The sensitivity of λ to changes in matrix elements (a_{ij}) simply describes the slope of λ as a function of a_{ij} or lower-level vital rates (x_{ij}). The elasticity of λ to a_{ij} or x_{ij} is the slope of log λ as a function log a_{ij} or x_{ij} (Caswell 2001). I used elasticities to describe the relative effect of matrix elements and lower-level vital rates on λ. Elasticities with greater values were interpreted as having greater influence on population change compared with other vital rates with lower elasticity values. Following convention, subscript *i* and *j* describe the *i*th row and *j*th column in matrix A.

Retrospective Population Response

I used a life table response experiment (LTRE, Caswell 2001) to quantify the influence of landscape D on λ. The LTRE describes the contribution of vital rates from landscape D on population growth for the mean matrix ($A^{\bullet}$). The term experiment is used in a general context in this literature and includes comparisons between observational data (Caswell 2001). The mean matrix is defined as [$A^{\bullet} = (A^{D} + A^{C}) / 2$] where A is a matrix, superscript period signifies the mean matrix, and superscript D and C refer to landscape type. The difference in $\lambda^{\bullet} - \lambda^{C}$ is the contribution of sub-populations from landscape D to $\lambda^{\bullet}$. The sum difference in the contribution of lower-level vital rates to $\lambda^{\bullet}$ was approximated from the equation

$$\lambda^{\bullet} - \lambda^{C} = \sum (x_{ij}^{\bullet} - x_{ij}^{C}) \frac{\partial \lambda}{\partial x_{ij}} .$$

In effect, the difference between vital rate values ($x_{ij}^{\bullet} - x_{ij}^{C}$) was multiplied by the mean matrix sensitivity for that vital rate ($\frac{\partial \lambda}{\partial x_{ij}}$) (Levin et al. 1996, eqn 10.19 from Caswell 2001, Hagen 2003). Hence, the values within the summation estimate the contribution of particular vital rates from landscape D on population growth. In slightly different terms, these values approximate the sensitivity of $\lambda^{\bullet}$ to the contribution of specific vital rates from landscape D.

Management Simulations

Evaluating the response of λ to "what if" scenarios is an approach that can point out gaps in data knowledge, or help prioritize management alternatives (Beissinger and Westphal 1998, Caswell 2000, Fieberg and Ellner 2001). Therefore, given the findings from the LTRE analysis, I was interested in evaluating the amount of change in specific vital rates from sub-populations in landscape D to raise the probability of $\lambda \geq 1$ in at least 50% of the runs. I applied a life stage simulation analysis (LSA, Wisdom et al. 2000) by modifying the mean of specific vital rates, and re-estimating the associated SE and CI applicable to the matrix model (A^D). Vital rates subject to change were based on hypothetical scenarios that focused on hunting and habitat management.

Hunting Scenario.—Hunting mortality has traditionally been treated as compensatory to other forms of mortality for r-selected game birds such as grouse. More recently, some evidence has suggested hunting may be additive to other forms of mortality, particularly in declining populations (Johnson and Braun 1998). Compensatory mortality occurs through some form of density dependent process working to hold a population in check in the absence of harvest. While some grouse populations likely experience density dependent forces from intra-specific competition (Hannon 1983, Newton 1992, Moss et al. 1996, Matthiopoulos et al. 1998), I can find no evidence suggesting sharp-tails are limited in this manner. Indeed, evidence of density dependence in prairie grouse is largely unquantified. Therefore, my first management scenario was an increase in survival for hens (HENWINTER) and juveniles (JUV) due to a reduction in fall hunting. I changed the mean value of these vital rates by 10%, 15% and 20% to approximate changes in hunting mortality (Johnson and Braun 1998, Hagen 2003). I speculate that 10% or 15% increases in survivorship may occur as a function of reduced daily or seasonal bag limits, while a 20% reduction in mortality may occur if hunting is closed or severely restricted (i.e. pre-set limit of tags). To the best of my knowledge, there are no data available from this region to estimate these values. Therefore, in the absence of empirical data, juvenile and adult females were assumed to be equally vulnerable to mortality from hunting.

Habitat Scenario.—The second management scenario assumed the height of concealment cover could be managed during the nesting period (1 May to 15 July). I assumed that nest success would improve as a function of increasing the height of concealment cover (Chapter 2). I applied a logistic equation that related the benefit of concealment cover height measured over a 50-m scale near the nest (model 5C from Table 2-4, chapter 2) such that

$$\text{nest success probability} \approx \frac{e^{-1.82 + (0.19)(\text{concealment cover})}}{1 + e^{-1.82 + (0.19)(\text{concealment cover})}}.$$

I assumed that concealment cover could be managed at low, moderate and tall heights by management treatments. I quantified these categories based on visual obstruction readings (VOR) measured at nests in the study area (90% of range, Chapter 2), such that low VOR ranged from 3–9 cm, moderate was 6–13 cm, and tall was 9–20 cm. The value of concealment cover for each treatment of each replicate was randomly selected from a uniform distribution within the given range. Values for the other vital rates were randomly selected from the 95% CI range from the original data for landscape D. I applied the habitat management scenario initially with concealment cover height affecting nest success alone, and in a second set of models improving both nest success and hen survivorship over the breeding season (HENBREED). I assumed that concealment cover that benefited nest success would also benefit hen survivorship during nesting such that high, moderate and low concealment cover equated to flat, 5% and 10% upward adjustments to the mean for HENBREED.

Hunting and Habitat Scenario.—The third LSA combined the previously described modifications from the Hunting and Habitat scenarios to account for changes in 4 vital rates (NEST, JUV, HENBREED, HENWINTER). The change in values was identical to that for each scenario described above. Hence, these scenarios assume hunting restrictions were applied, and habitat was managed for target concealment cover heights (from light, moderate and heavy grazing) at the 50-m scale.

RESULTS

Apparent nest success was 0.47 ± 0.02 ($\bar{\chi}$ ± SE) based on 107 nest events from individual hens from 1999–2001. Nest success was substantially higher in landscapes with less crop and sparse grassland (Table 5-1). Clutch size averaged 11.79 ± 0.25 for first nests and re-nests pooled together. The proportion of eggs hatched per successful nest was 0.95 ± 0.01. A summary of parameter values with their 95% CI is in Table 5-1. Seasonal rainfall was greater than average in 1999, and lower than average in 2000 and 2001 (Appendix 2 Fig. A-2-1).

The population matrices differed substantially between sub-populations from landscape D and landscape C. The upper-level matrix elements were

$$\text{Landscape D} = \begin{bmatrix} 0.453 & 0.453 \\ 0.363 & 0.363 \end{bmatrix} \quad \text{Landscape C} = \begin{bmatrix} 0.978 & 0.978 \\ 0.500 & 0.500 \end{bmatrix}$$

The mean rate of population growth was lower in landscape D ($\lambda^D = 0.7520$) compared with C ($\lambda^C = 1.3850$), and ranged above 1 in fewer bootstrap replicates (14% and 76% respectively). The relative importance of adult survival compared with reproductive contributions to population change differed between the 2 landscapes. The elasticity of λ to reproductive vital rates (x_{ij}) was lower in landscape D (0.525) compared with C (0.633), while elasticity to adult survival (x_{ij}) was greater in D (0.475) compared with C (0.367). Adults comprised a greater portion of the stable age distribution (right eigenvector) in landscape D (48%) compared with C (37%).

Population growth summed over the entire study area returned an estimated $\lambda \geq 1$ in 43% of the 1,000 bootstrap replicates based on a mean value very close to 1 ($\lambda = 0.9998$, 95% CI 0.5667–1.5333). The relative effects (elasticity) of reproductive vital rates (0.572) were moderately greater than for adult female survival (0.428).

Retrospective Population Response

Landscape D had a negative overall contribution to population growth for the study population ($\lambda^{\bullet} - \lambda^C = -0.350$). The LTRE suggested that population growth ($\lambda^{\bullet}$) was particularly sensitive to the negative contribution of lower nesting success in landscape D compared with C (Fig. 5-1). Lower survival of hens over the breeding season and lower chick survival also had negative relative effects on the contribution to λ^* (Fig. 5-1).

Management Simulations

Hunting Scenario.—Reducing the mortality of juveniles and hens from reductions in hunting bag limits increased population growth in a near linear pattern. However, even with an increase in both these vital rates by 20%, λ^D only achieved a value ≥ 1 in 35% of the 1,000 replicates (Fig. 5-2). Therefore, sub-populations in areas with $\geq$ 35% crop and sparse grassland would likely decline, or possibly rely on immigration to maintain numbers over time.

Habitat Scenario.—Concealment cover height ranging from 3–9 cm produced a mean λ^D value of 0.755, with values ≥ 1 in 15% of the 1,000 replicates (Fig. 5-3A). This pattern was similar to the results from the original matrix values for A^D. The rate of population change was ≥ 1 in 58% of the replicates when concealment cover was managed for the taller cover range (9–20 cm). The scenario managed for the mid-range of cover values (6–13 cm), produced an average growth estimate below 1 (λ^D = 0.947), and fell short of my target for the number of replicates above 1 ($\lambda^D \geq 1$ = 37%, Fig 5-3A). Factoring in greater hen survival over the breeding season had a moderately positive effect on λ in addition to the benefit of improved nest success (Fig. 5-3B). The rate of population change increased above 1 ($\lambda^D \geq 1.184$) for the management scenarios that provided concealment cover heights that ranged between 9 and 20 cm.

Hunting and Habitat Scenario.—The combined effects of hunting and habitat management returned target values for λ^D with smaller changes in vital rates (Fig. 5-

4). Managing for cover heights ranging from 6–13 cm, and hunting restrictions that curb juvenile and adult mortality by 15% resulted in a mean value >1 for population change ($\lambda^D = 1.100$), with 55% of the replicates in positive growth (Fig. 5-4). This suggests that λ^D is relatively sensitive to management scenarios that provide relatively small positive changes to the 4 vital rates (NEST, JUV, HENBREED, HENWINTER).

DISCUSSION

I had 4 main findings. First, the rate of population change was negative in disturbed landscapes and positive in continuous habitats suggesting landscape scale habitat patterns can be linked to population growth. Second, the rate of population change was very sensitive to changes in reproductive vital rates, and in particular nesting success. Nest success differed markedly between the 2 landscape types suggesting nests are much more vulnerable in disturbed landscapes. Third, a reduction in hunting related mortality is unlikely to have a large enough impact to increase population growth above 1 in disturbed areas. And finally, habitat managed for greater concealment cover to improve nest success and reduce hen mortalities had the largest relative effect on population growth in disturbed landscapes.

Scale and λ Estimates

Estimates of population change are relevant to the spatial scale used for the investigation. Most female grouse nested within an 8-km^2 breeding complex around lek sites (Chapter 2), and I subsequently measured reproduction and survival through the various life stages at this scale. Therefore, the λ found should be interpreted at this scale. This system appears to have areas that provide an abundance of recruits (landscape C), and areas unable to sustain numbers without immigration of new recruits (landscape D). In effect, a source/sink dynamic is likely occurring in this region at the scale of the breeding complex (sensu Pulliam 1988). However, I did not measure survival of juveniles beyond 30-days post-hatch nor the spatial movement of recruits into the breeding population, so direct evidence of a source/sink dynamic is lacking.

I caution interpretation of these results as a measurement of λ beyond the scale of the breeding complex. I believe my selection of individuals used to measure vital rates was random at the scale of the lek, but my choice of the leks used to capture female grouse was not random. Capture leks were chosen based on the composition of habitat within a 1,600-m radius and included leks that gave a range for crop at this scale. I did not know the location of all the leks in the study area, and those known were likely biased towards those easy to locate while traveling on a road. Hence, I do not imply the region has equal proportions of disturbed and continuous habitat at the scale relevant to my measurement of population growth near leks. Therefore, estimates of λ should be interpreted at the 8 km^2 scale, rather than drawing conclusions about population growth over the entire study area.

Vital Rate Bias

Sampling error, or insufficient years to capture the range in normal variation for vital rates may bias these models (Beissinger and Westphal 1998). These data were derived from 3-years of study, which may not account for the natural variation that occurs in vital rates in this system. To mitigate against possible shortfalls in the time-span of data collection I used a uniform distribution to draw upon for vital rates.

A uniform distribution does not favor a mean value over any other within the specified range and therefore presumably returns a broader range of values. Further, the potential for overstating survival estimates increases as the proportion of right censoring increases, particularly if sample sizes are relatively small (i.e. $n \leq 50$ individuals, Tsai et al. 1999, Hagen 2003). The sample size used in survival estimates for chicks to 30-days post-hatch was less than 50 for both landscapes types, and censoring was approximately 34%. Hence, the mean estimate for this vital rate could be overestimated; however, the SE associated with these estimates is relatively large, resulting in broad confidence intervals. Again, the use of a uniform distribution should mitigate the risk associated with overestimating mean survival value. Survival estimates within the 95% CI for chicks cover the range of values reported by the only other comparable study on a galliforme (Riley et al. 1998).

I am confident with the estimates of hen survival over the breeding season. Sample sizes were close to 50 ($n = 46$, $n = 65$), and less than 13% of the data were censored. I am also confident with the estimates for nest success, which are similar to other estimates for sharp-tails (Bousquet and Rotella 1998, Roersma 2001). I used similar telemetry methods as another study in southwestern Alberta (Roesrma 2001), although my approach was presumably less intrusive as I did not mark nest areas with a flag nor flushed sitting hens to count eggs. Success of nests in continuous landscapes (0.68 ± 0.05) in the study area was similar to that for Roersma's entire study site (0.65). His study area was mostly a large continuous block of grassland habitat (27 km^2).

Over-winter survival may be biased high since the sample size was near 50 (n = 52), and 46% of the individuals were right censored. I did not track birds over-winter and hence only used a return rate of the number of individuals found the following spring to calculate this parameter. Since I did not monitor hens weekly or monthly, individuals censored as a result of radio failure was likely. Further, annual estimates of hen survival for sharp-tails and their congeners are in the range I report (Connelly et al. 1998, Giesen 1998, Hagen 2003), which suggests that these data are reasonable. Estimates of juvenile survival (JUV) were based on data from a prairie system in Kansas, and therefore may not be representative of the Alberta system. Notwithstanding the potential biases associated with over-winter hen survival and juvenile survival, these were the best data available for this model at this time. Future work that verifies estimates for these 2 rates will help validate model predictions.

Retrospective Population Response

The retrospective LTRE indicates a negative contribution of population change from landscape D on the entire study population. Population growth for the mean matrix was most sensitive to the negative contribution of lower nest success from landscape D. The high relative influence of nest success is consistent with other studies on short-lived grouse that have shown the rate of population change most sensitive to reproductive vital rates (Wisdom and Mills 1997, Peterson et al. 1998). Conversely, adult survival often has a stronger relative effect in species of grouse and waterfowl with greater adult survival rates (Schmutz et al. 1997, Flint et al. 1998, Johnson and Braun 1998). However, the relative effect of hen survival

(HENBREED, HENWINTER) on population change differed between landscapes in this system, demonstrating that elasticity values are subject to changes in 1 or more vital rates (Mills et al. 1999). The elasticity of hen survival increased as population change shifted from a positive (λ^C) to a negative rate (λ^D). In effect, the influence of hen survival on population growth became more important as the estimate of λ decreased in value from λ^C to $\lambda^\bullet$ to λ^D. Hence, management alternatives that address this rate seemingly become more relevant in landscapes with lower population growth in this system (i.e. in more disturbed areas).

Management Simulations

The prospective LSA demonstrated the relative change necessary in particular vital rates to effect positive change in λ for sub-populations in landscape D. A relatively large change (>20%) would be required to attain a stable λ value by adjusting hunting mortality alone. However, I do not know the actual mortality from hunting within this population and only had 1 hen confirmed as a hunter kill over the 3-year study. I did not monitor hens or juveniles over the hunting season or winter months so estimates of these parameters do not differentiate hunter caused deaths. These data would be helpful in order to quantify the relative effect of hunter kills on λ. However, in the absence of evidence suggesting λ is held in check by density dependence, and the increasing elasticity of λ to adult survival, hunting may have an additive affect in more disturbed landscapes.

Managing concealment cover near nests resulted in positive λ values in at least 50% of the bootstrap runs when managed for heights ranging from 9–20 cm. This was the range in concealment cover height for the upper 50% of nests (Chapter

2) and therefore is presumably realistic as a management objective. Hens clearly demonstrated selection for nesting areas with more concealment cover at the 50-m scale (Chapter 2), so managing grasslands for homogenous VOR heights in this range may not be possible given normal variation in soil and moisture regimes. Precipitation plays a strong role in annual vegetation height (Higgins and Baker 1982), so managing grasslands while accounting for patterns in precipitation over years is important. Indeed, mean annual precipitation values can be misleading if an area commonly goes through years of periodic drought punctuated by occasional very wet years (skewed distribution, Boyce 1992). Ideally, management treatments that influence the height of concealment cover should be done with drought years as a baseline, rather than using vegetative growth based on mean values as a guide.

Management models that incorporated concealment cover relied on the logistic function that links cover height to nest success. This model by definition follows a logistic curve with very tall cover heights having diminishing positive effects on nest success. Other studies have suggested having too much cover around a nest site can lead to deleterious effects because hens become more vulnerable to mortality if they cannot detect predators early enough to escape (Wiebe and Martin 1998). My models suggest taller dense cover was not a negative influence on nest success in this system (Chapter 2). In theory, given a broader range of concealment cover height, nest success may be negatively influenced at very high cover heights. In practice, this is unlikely to be a serious management concern in Mixed and Dry Grass Prairie systems that are grazed annually.

Comparatively small changes in the range of values of 4 vital rates predicted a positive growth rate in more than 50% of the runs (Fig 5-4.). This illustrates the benefit of management alternatives that have the potential to influence more than 1 vital rate at once. Indeed the model predicts that λ^F can achieve average values ≥ 1 with more than 50% probability using mid-range cover heights (6–13 cm), if coupled with reduced hunting. Hence, the option of reduced hunting may be particularly valuable in areas where habitat conditions are marginal for achieving taller concealment cover heights (e.g. 9–20 cm). This may be applicable in areas with natural soil and moisture regimes that severely limit growth, or areas degraded through grazing or other forms of land conversion over the years. Reductions in hunting related mortality could be used in conjunction with grass management until such time that concealment cover heights reach target levels through most years.

The factors linked to differences in the rates of nest success are not fully known, but likely extend beyond the amount of concealment cover within 50-m of a nest. Predators cause the failure of nests for most prairie grouse (Schroeder and Robb 1993, Connelly et al. 1998, Giesen 1998, Schroeder et al. 1999), but the habitat features linked with greater nest predation vary with scale. Habitat disturbance by humans has been linked with changes in predator density, predator search efficiency, and even shifts in the community of predators (Kurki et al. 2000, Andrén 1992, Chapters 2 and 3). I demonstrated that crow density was greater in landscapes with more crop and sparse grassland (8 km^2), and found lower success for grouse nests in areas with greater corvid density (Chapter 2). In a similar manner, fox densities were greater in landscapes with more crop and pastureland in Finland (Kurki et al. 1998).

The authors linked greater fox densities in these disturbed landscapes with lower breeding success for black grouse (*Tetrao tetrix*) and capercaillie (*T. urogallus*) (Kurki et al. 2000). Hence, the density of generalist predators can increase in disturbed landscapes at scales relevant to the predator in question. Further, fragmenting nesting habitat into smaller patches can benefit predators by reducing the amount of space to be searched, thus improving their searching effort (Pasitschniak-Arts et al. 1998). Habitat features that aid predator detection of prey can also occur at very small spatial scales. For example, trees encroaching into the prairies may provide a resource to avian predators that use perches to locate nests (Paton 1994, Chapter 2). Therefore, the benefit of nesting cover may be overshadowed by other factors influencing the density and efficiency of generalist predators. I attempted to factor in broad-scale habitat patterns associated with nest (corvids) and sharp-tail hen predators (raptors) by using the scale of habitat associated with their relative densities (Chapters 2 and 3). So while the function between concealment cover and nest success is a naive model, it forms a foundation to build upon as a management tool that incorporates scales relevant for predation related to this prey species.

Management Implications

As a starting point for managing sharp-tails in prairie landscapes, I suggest habitat be characterized at scales relevant to breeding sub-populations. These data suggest areas with $\geq$35% crop and sparse grassland at 8 km^2 extents have a greater probability of a declining growth rate compared to areas with <35%. Hence, requests for land conversion from perennial grass to crop in areas near or below that 35% threshold should be weighed carefully. A recent initiative by the Canadian federal government seeks to promote sustainable land use and biodiversity by converting marginal cropland into perennial cover. The Greencover Canada program has similarities to the Conservation Reserve Program in the USA by providing financial subsidies to landowners. These models can provide guidance for land managers set with the task of prioritizing the plots of land targeted for conversion back to perennial grass. Plots can be ranked while evaluating the scale and habitat composition important for sharp-tails. Further, my simulation of the relationship between concealment cover and vital rates (nest success, hen survival over the breeding season) can provide target cover heights to achieve in these renewed grasslands. I recommend that targets for concealment cover height are in the upper range (9–20 cm), and that subsequent study be carried out to evaluate the predictive model.

These management simulations used hypothetical estimates of the mortality associated with hunting in this region (10–20%). Taking a precautionary approach, hunting mortalities should be quantified in this system given the increasing vulnerability of λ to these life stages in disturbed areas. For similar reasons, these models would benefit from additional data to parameterize over-winter survival for hens and juveniles in this system. Hence, I present these simulation results as working models that will benefit from data gathered over additional years to better estimate the distribution of the variation around vital rates.

Table 5-1. Mean parameter estimates of vital rates for sharp-tailed grouse across the entire study area, and for vital rates derived separately from individuals in landscapes with < 35% crop and sparse grassland (C) vs. ≥ 35% (D).

Vital rate	$\bar{\chi}$	n	95% CI	$\bar{\chi}$	n	95% CI	$\bar{\chi}$	n	95% CI
	entire study area			landscape C			landscape D		
CLUTCH	11.79	72	11.31-12.28						
HATCH	0.952	46	0.925-0.979						
SEX	0.50[a]								
NEST	0.468	107	0.373–0.562	0.683	41	0.575-0.791	0.348	66	0.238-0.407
CHICK	0.406	70	0.250-0.570	0.418	46	0.123-0.714	0.380	24	0.117-0.642
JUV	0.539	32[b]	0.365-0.713						
HENWINTER	0.807	52	0.794-0.821						
HENBREED	0.533	111	0.435-0.631	0.620	46	0.483-0.757	0.450	65	0.313-0.587

[a] Assumed 1:1 sex ratio.

[b] Based on survival estimates for lesser prairie-chicken juveniles (Hagen 2003).

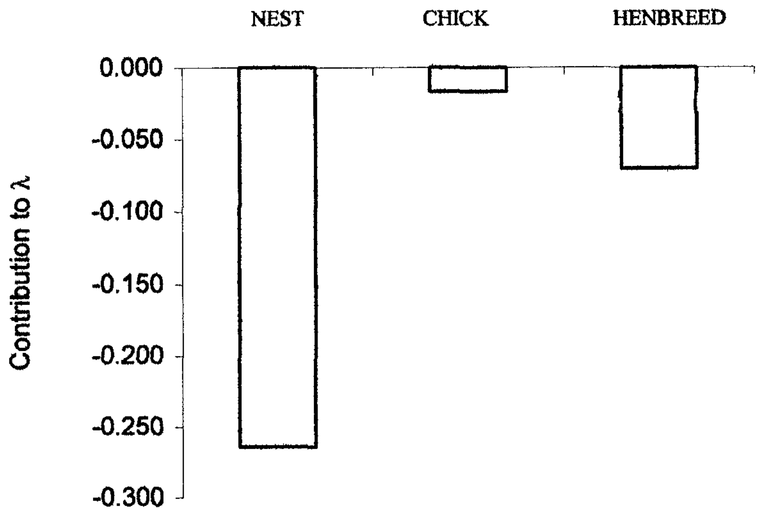

Fig 5-1. Contribution of vital rates for nest success, early chick survival, and hen survival over the breeding season from landscape D on population growth for the mean matrix ($A^{\bullet}$). Negative values suggest vital rates from landscape D had a negative contribution on population growth compared with values for these vital rates from landscape C.

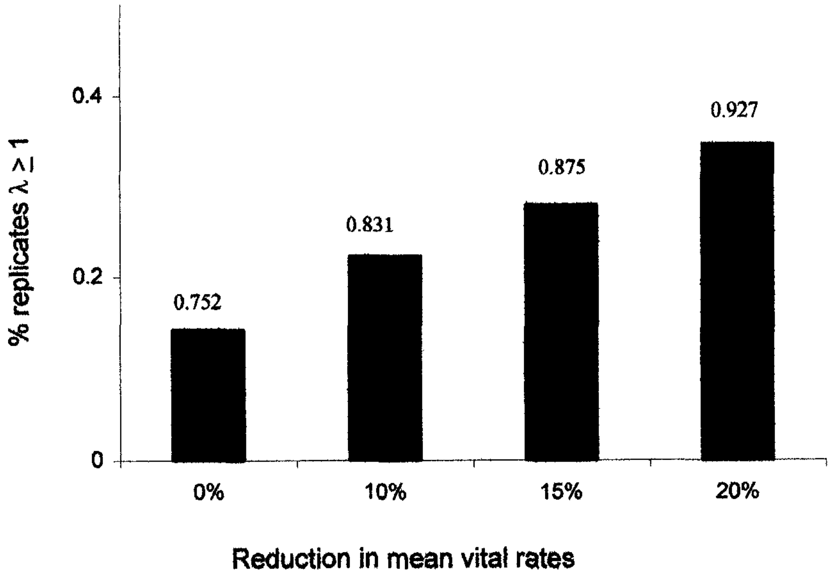

Fig. 5-2. Proportion of times $\lambda \geq 1$ in 1,000 resampled replicates of a stochastic demographic model for sharp-tailed grouse based on vital rates derived in landscapes with $\geq$ 35% crop and sparse grassland. Mean survival of juveniles and breeding aged females increased 10, 15, and 20% by hypothetically reducing mortalities during fall through reduced hunting bag limits. The mean λ value for 1,000 bootstrap replicates is above bars.

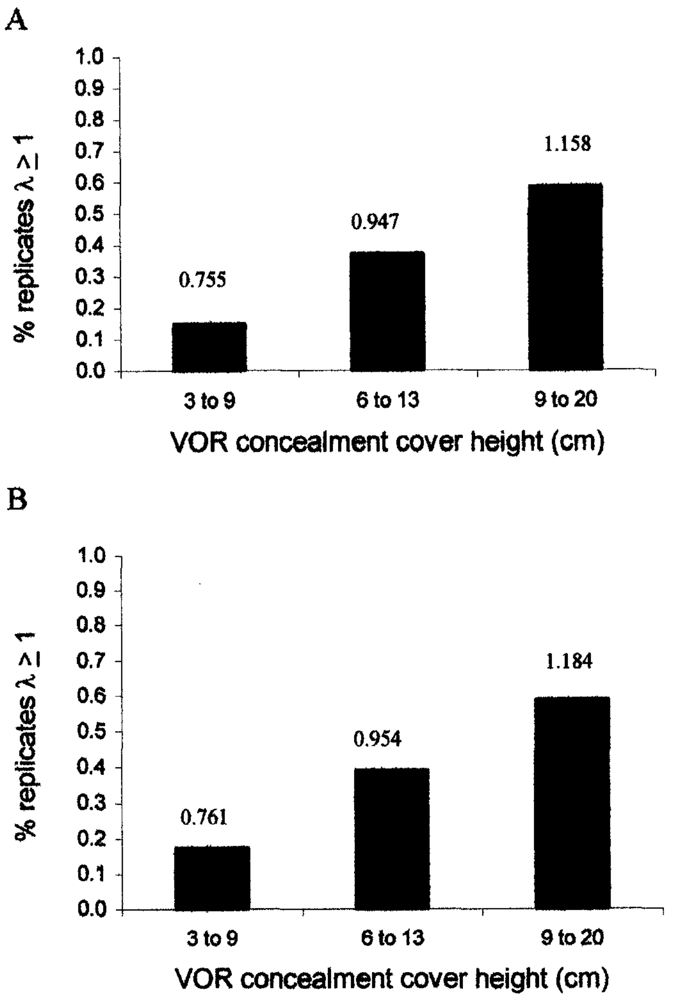

Fig. 5-3. Proportion of times $\lambda \geq 1$ in 1,000 replicates of a stochastic model for sharp-tailed grouse based on vital rates derived from landscapes comprised of ≥ 35% crop and sparse grassland. A) Mean nest success (NEST) increased as a function of concealment cover within 50 m of nests. Logistic function between nest success and concealment cover height (VOR) described in text. B) Mean nest success and survival of hens during the breeding season increased as a function of concealment cover. Hypothetical treatments managed the range of concealment cover height (cm). The mean λ value for 1,000 bootstrap replicates is above bars.

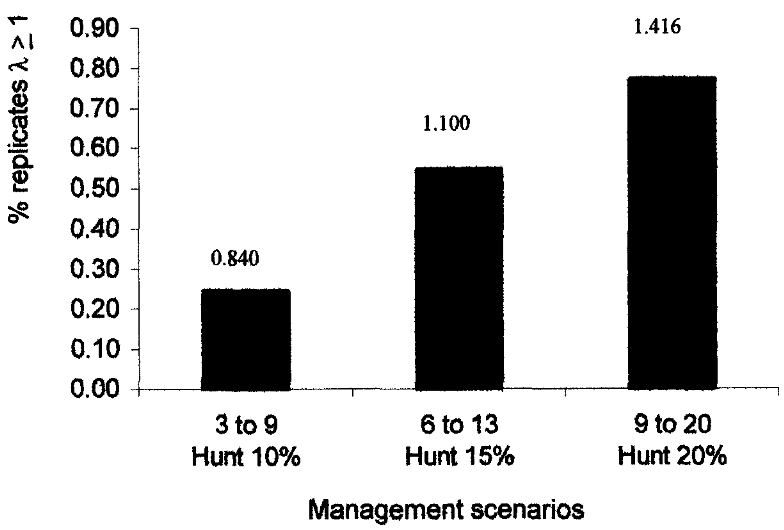

Fig. 5-4. Proportion of times $\lambda \geq 1$ in 1000 resampled replicates of a stochastic demographic model for sharp-tailed grouse based on vital rates derived in landscapes with $\geq$ 35% crop and sparse grassland. Two management treatments applied for 3 scenarios (y axis). Hunt treatment: mean survival of juveniles and breeding aged females increased 10, 15, and 20% by hypothetically reducing mortalities during fall through reduced hunting bag limits. Habitat treatment: Mean nest success (NEST) and survival of hens during breeding season increased as a function of the range of concealment cover height (cm) within 50 m of nests. The mean λ value for 1,000 bootstrap replicates is above bars.

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CHAPTER 6

MANAGEMENT BRIEF

Management alternatives for sharp-tails should be prioritized in the context of spatial scale. Efforts to improve small-scale processes such as concealment cover for nests, or removing perch sites may have limited success without considering larger scale factors associated with predator densities. Therefore, a plausible initial step is to identify areas with strong vs. weak potential for stable population growth by quantifying habitat composition at the scale of the breeding complex for sharp-tails (8 km^2, continuous vs. fragmented, Chapter 5). Areas near the margin of 35% crop and sparse grassland can be prioritized for broad scale management. Hence, programs such as Greencover Canada can prioritize these marginal landscapes for converting cropland back into perennial grass.

Management alternatives at smaller scales should be directed toward landscapes identified as having good potential for stable growth. Annual population density was very elastic to nest success, so efforts that improve this life stage should provide optimal benefits. I suggest that the height of concealment cover be managed at the 50 m scale as this extent had a much stronger association with nest success than at the 2 m extent. Moreover, cover heights that average in the range from 9 to 20 cm have good potential for increasing nest success (Chapter 2, Chapter 5). The effect of trees on nest success was not made clear in this study but evidence suggests tree encroachment may be a problem, and therefore this relationship should be pursued in future work.

Mortality associated with hunting is not well known in this region. Determining the impact of hunting on annual population density is important for clarifying the benefits that can be gained by manipulating hunting regulations. This is particularly relevant in more disturbed landscapes where population growth is more sensitive to adult female mortality.

APPENDIX 1

An artificial nest experiment was conducted in June 1999. Pheasant eggs (n =11) and 1 dummy egg were placed at 77 nest sites at random locations across the study area. Placement of nests was stratified at the 2 m scale to compare nests with high (20-30 cm) vs. low (8 –12 cm) concealment cover. Concealment cover height was measured from a distance of 2 m away using a Robel pole (Robel et al. 1970). Nests were left out for 23-25 days before determining fate. Two devises were used to help identify predators as mammalian vs. avian; 1) A dummy egg formed from unfired porcelain clay was molded around one end of a 20 cm string. The string was tied to a long nail (8 cm) that was pushed in the ground under the nest; and 2) A hair catcher (Pasitschniak-Arts and Messier 1995) was formed by fitting sticky brown tape to a wire loop that was placed 6-8 cm over the nest bowl. The experiment had a high rate of nest predation (95%), and enabled me to differentiate between mammalian and avian predators in 68% of the cases. Evidence suggested avian species (corvids) were the primary predators (81%).

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APPENDIX 2

WEATHER DATA

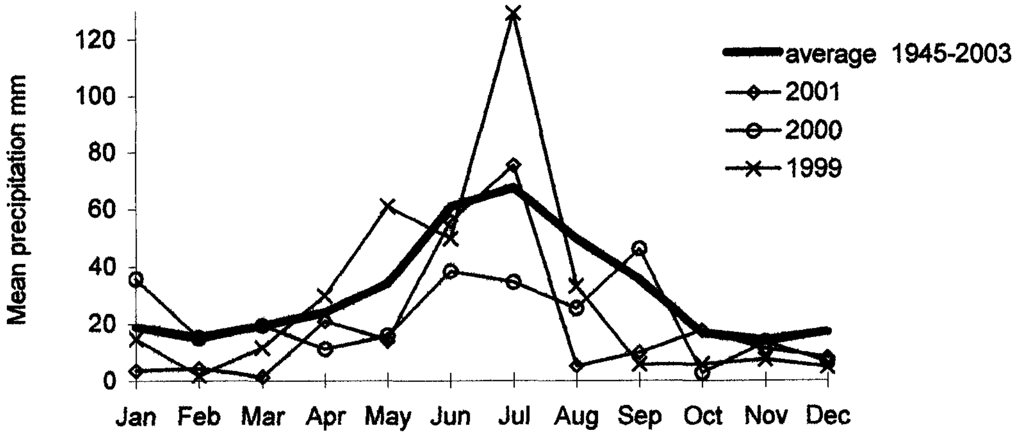

Fig. A-2-1. Annual precipitation at Coronation, Alberta averaged from 1945–2003, and for 1999, 2000, and 2001 separately. Annual precipitation was 96% in 1999, 71% in 2000, and 61% in 2001 with respect to the long-term average (371 mm, 1945–2003, Environment Canada).

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Environment Canada, Meteorological Service of Canada , National Archives and Data Management Branch, Downsview, Ontario.

APPENDIX 3

SUMMARY HABITAT DATA

Table A-3-1. Characteristics of habitat classified with GIS for the study area in southeastern Alberta.

Variable	Description
Tree	Tree and woody vegetation > 3 m tall.
Crop	Cropland, tilled fields, hay land cut annually, anthropogenic.
Dense grassland	Perennial grassland and shrub.
Sparse grassland	Perennial grassland and shrub with more bare ground reflectance than dense grassland. Daubenmire readings > 25% bare ground.
Wetland	Ephemeral wetland.
Water	Water.

Table A-3-2. Range and mean (± SE) for vegetation characteristics at 67 nest locations at 3 extents for sharp-tailed grouse in Alberta, 1999–2001.

Variable	Description	extent (m)	range	mean
Vor2	concealment cover height	2	7–57 cm	24 cm (1)
Overhd	cover over nest bowl	<1	0–100%	33% (3)
Bd2	bare ground	2	1–85%	7% (4)
Res2	residual cover	2	3–98%	60% (10)
Vor50	concealment cover height	50	1–34 cm	11 cm (0.8)
Bd50	bare ground	50	1–85%	19% (4)
Res50	residual cover	50	1–98%	55% (5)
Tree	composition	50	0–100%	13% (3)
Sparse grassland	composition	50	0–100%	20% (4)
Dense grassland	composition	50	0–100%	58% (4)
Wetland	composition	50	0–20%	<1% (<1)
Water	composition	50	0	0
Crop	composition	50	0–100%	9% (3)
Tree	composition	437	0–50%	7% (1)
Sparse grassland	composition	437	0–80%	25% (3)
Dense grassland	composition	437	2–87%	54% (3)
Wetland	composition	437	0–16%	<1% (<1)
Water	composition	437	0–29%	1% (<1)
Crop	composition	437	0–93%	11% (3)

Table A-3-3. Range in the proportion (%) of habitat composition within 1600 m of 16 leks used to capture sharp-tailed grouse hens in southeastern Alberta from 1999–2001.

Habitat type	range	$\bar{\chi}$	se
Trees	<1 – 16	5	(1)
Crop	<1 – 41	14	(4)
Sparse grassland	5 – 51	30	(3)
Dense grassland	26 – 70	48	(3)
Wetland	<1 – 9	3	(1)
Water	<1 – 4	1	(<1)
Crop + Sparse grassland	21 – 70	43	(7)

Table A-3-4. Range and mean (± SE) for vegetation characteristics at 40 sharp-tailed grouse brood locations for 2 spatial extents in Alberta, 1999–2001.

Variable	Description	extent (m)	range	$\bar{x}$	se
Vor50	concealment cover height	50	<1–34cm	12	(1)
Bd50	bare ground	50	1–85%	33	(8)
Res50	residual cover	50	1–98%	50	(8)
Tree	composition	50	0–60%	8	(2)
Sparse grassland	composition	50	0–99%	21	(5)
Dense grassland	composition	50	0–99%	51	(6)
Wetland	composition	50	0–40%	3	(2)
Water	composition	50	0–20%	1	(<1)
Crop	composition	50	0–99%	17	(6)
Tree	composition	583	0–42%	9	(2)
Sparse grassland	composition	583	2–72%	22	(3)
Dense grassland	composition	583	20–81%	53	(2)
Wetland	composition	583	0–11%	3	(<1)
Water	composition	583	0–18%	2	(1)
Crop	composition	583	0–65%	12	(3)

Table A-3-5. Range in the proportion (%) of habitat composition at 26 avian predator survey locations at 2 extents in southeastern Alberta.

Habitat type	range	$\bar{x}$	se	range	$\bar{x}$	se
	1600 m			2265 m		
Trees	1–16	4	(1)	1–14	5	(1)
Crop	0–56	25	(4)	1–49	26	(3)
Sparse grassland	5–70	25	(3)	8–62	24	(3)
Dense grassland	22–81	43	(3)	25–76	42	(3)
Wetland	<1–9	2	(<1)	1–8	2	(<1)
Water	<1–4	1	(<1)	<1–2	1	(<1)
Crop + Sparse grassland	10–74	50	(4)	16–70	50	(3)