

THE INFLUENCE OF FINE-SCALE HABITAT FEATURES ON REGIONAL VARIATION IN POPULATION PERFORMANCE OF ALPINE WHITE-TAILED PTARMIGAN

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Abstract. It is often assumed (explicitly or implicitly) that animals select habitat features to maximize fitness. However, there is often a mismatch between preferred habitats and indices of individual and population measures of performance. We examined the influence of fine-scale habitat selection on the overall population performance of the White-tailed Ptarmigan (*Lagopus leucura*), an alpine specialist, in two subdivided populations whose habitat patches are configured differently. The central region of Vancouver Island, Canada, has more continuous and larger habitat patches than the southern region. In 2003 and 2004, using paired logistic regression between used ($n = 176$) and available ($n = 324$) sites, we identified food availability, distance to standing water, and predator cover as preferred habitat components. We then quantified variation in population performance in the two regions in terms of sex ratio, age structure ($n = 182$ adults and yearlings), and reproductive success ($n = 98$ females) on the basis of 8 years of data (1995–1999, 2002–2004). Region strongly influenced females' breeding success, which, unsuccessful hens included, was consistently higher in the central region ($n = 77$ females) of the island than in the south ($n = 21$ females, $P = 0.01$). The central region also had a much higher proportion of successful hens (87%) than did the south (55%, $P < 0.001$). In light of our findings, we suggest that population performance is influenced by a combination of fine-scale habitat features and coarse-scale habitat configuration.

Key words: *Lagopus leucura*, grouse, alpine, resource selection, habitat use, White-tailed Ptarmigan, fragmentation, metapopulation.

Influencia de Características del Hábitat a Escala Fina sobre la Variación Regional del Desempeño Poblacional de *Lagopus leucura*

Resumen. Frecuentemente se asume (explícita o implícitamente) que los animales seleccionan características de hábitat de forma de maximizar su adecuación biológica. Sin embargo, en muchos casos existe una divergencia entre los hábitats preferidos y los índices que miden el desempeño de individuos y poblaciones. Examinamos la influencia de la selección de hábitat a escala fina sobre el desempeño general de la población de *Lagopus leucura*, un especialista alpino, en dos poblaciones subdivididas en las que los parches de hábitat tienen una configuración espacial diferente. La región central de la Isla Vancouver, Canadá, tiene parches de hábitat más continuos y de mayor tamaño que las regiones que se encuentran más al sur. En 2003 y 2004, utilizando una regresión logística pareada entre sitios usados ($n = 176$) y disponibles ($n = 324$), identificamos la disponibilidad de alimento, la distancia a un cuerpo de agua estancada y la cobertura ante depredadores como componentes preferidos del hábitat. Luego cuantificamos la variación en el desempeño de la población en las dos regiones en términos de cociente de sexos, estructura de edades ($n = 182$ adultos y juveniles de un año) y éxito reproductivo ($n = 98$ hembras) con base en 8 años de datos (1995–1999, 2002–2004). La región influyó fuertemente el éxito reproductivo de las hembras, el cual, incluyendo los individuos no exitosos, fue consistentemente mayor en la región central ($n = 77$ hembras) de la isla que en el sur ($n = 21$ hembras, $P = 0.01$). La región central también tuvo una mayor proporción de individuos exitosos (87%) que la del sur (55%, $P < 0.001$). A la luz de nuestros resultados, sugerimos que el desempeño poblacional es influenciado por una combinación de las características del hábitat a escala fina y la configuración del hábitat a escala más gruesa.

INTRODUCTION

It is often assumed that animals' selection of particular habitat components is driven by the fitness consequences of selection (Martin 1998, Manly et al. 2002). The selection of habitat components refers to the disproportionate use of available habitats and can reflect the variability and importance of resources;

it can take place at multiple spatial scales (Orians and Wittenberger 1991, Johnson et al. 2004, Anderson et al. 2005, Chalfoun and Martin 2007). Fine-scale selection is examined at the level of immediate influence and refers to the decisions an animal makes as it moves throughout the landscape, selecting specific characteristics. These fine-scale habitat-selection decisions can influence an individual's survival (Patten et al. 2005) and

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reproductive success (Walters et al. 2002). However, it is often less clear how the distribution of fine-scale habitat features relates to overall population performance (e.g. survival, reproductive success). We studied the fine-scale habitat-selection behavior and population performance of the subspecies of the White-tailed Ptarmigan endemic to Vancouver Island (*Lagopus leucura saxatilis*) in two regions that differed in levels of habitat fragmentation.

Regional variation in population performance can be caused by variation in factors such as resource availability, predation, and competition. Understanding the realized influence of habitat structure on population performance begins with the identification of preferred habitat variables. After those variables are identified, examination of corresponding regional variation in key habitat variables may elucidate which components of the habitat have the greatest effect on population performance (Mauritzen et al. 2003, Ludynia et al. 2005). This information provides insight into the relationships among individual, fine-scale habitat selection and population-level processes.

The White-tailed Ptarmigan is an alpine grouse restricted to areas at or above the treeline throughout the year (Martin et al. 2004). Our research was done in the central (continuous alpine habitat) and southern (smaller, more isolated alpine patches) regions of Vancouver Island. Telemetry ($n = 118$ individuals) detected no movement between these regions, but genetic data ($n = 113$ individuals) analyzed by Bayesian clustering methods showed connectivity and suggested that genetic variation was best explained by two clusters representing the two regions (Fedy et al. 2008).

Studies of the White-tailed Ptarmigan on the mainland (Colorado, Alberta) have documented the importance of food, moisture, and predation to the species' life history and habitat-selection behavior (e.g. Herzog 1977, Giesen and Braun 1992, Sandercock et al. 2005b). The birds also need to cool themselves in summer heat, as they are well insulated and adapted to cold environments (Johnson 1968). Thus three important components of the White-tailed Ptarmigan's habitat ecology could influence fitness or survival: (1) food availability, (2) predator avoidance, and (3) thermal regulation. On the basis of these needs we designed a priori hypotheses to identify important fine-scale habitat components. In addition, we examined variation in population performance (survival, reproductive success) between the central and southern regions. Landscape structure (e.g., patch area and isolation) and the composition of the surrounding matrix influence patch occupancy (Thomas and Jones 1993, Hanski 1998, Moilanen and Hanski 1998, Prugh et al. 2008). The probability of occupancy is lower in smaller, more isolated habitat patches (MacArthur and Wilson 1967). Patch occupancy can be influenced by the movement of individuals into and out of patches (connectivity; Prugh 2009) and the capacity of a local population to maintain its performance in terms of reproductive success and

survival. From theory and empirical evidence, we predicted that population performance should be lower in the southern region where the alpine habitat consists of smaller patches. We then examined whether the distribution of fine-scale habitat components corresponded to regional variation in population performance. In other words, can we scale up from individual-level choices and fine-scale habitat features to population-level processes?

METHODS

STUDY AREA AND FIELD METHODS

Vancouver Island, located off the coast of British Columbia, Canada, is the largest island on the North American west coast. It is ~ 460 km long (north to south) and 50–80 km wide (31 284 km²). We located White-tailed Ptarmigan by playbacks of males' territorial calls during the early breeding season (May–late June 1995–1999, 2002–2004) and by playbacks of chicks' distress calls later in the season (late June–October). We captured them with a noose pole (Zwickel and Bendell 1967) and outfitted them with a necklace radio collar (RI-2D/2B, 18-month battery life, weight 6–9 g, Holohil Systems, Ltd., Carp, Ontario) and colored leg bands. We aged the ptarmigan by the shapes of the 8th and 9th primaries and by the presence of pigmentation on the 9th and 10th primary coverts, which distinguishes first-year birds from older birds (Bergerud et al. 1963).

FINE-SCALE HABITAT SELECTION

We recorded fine-scale habitat-selection data on radio-collared birds during chick rearing (July–August 2003, 2004). Observers maintained sufficient distance (approximately 35 m) from focal birds to ensure minimal disturbance and used binoculars to record the birds' locations every 30 min over periods of 3 hr. Each period resulted in seven observations per bird (at 0, 30, 60, 90, 120, 150, 180 min). The duration of these sessions allowed time for birds to engage in a number of behaviors (feeding, vigilance, etc.), and select multiple sites from those available in the immediate area. Sessions were occasionally shortened because of weather or terrain. After a 3-hr observation ended, we recorded habitat data from a 20-m² plot (radius ~2.5 m) with the bird's location at its center. These locations represented *used* habitat, as the focal individual occupied it at the time (Jones 2001). We observed each individual bird for only one session each year (two birds were observed in both 2003 and 2004).

We constrained the selection of *available* sites to within an individual's territory to ensure that sites were available to individuals. Available sites, by definition, included all habitat types within the territory, including *used* habitats (Jones 2001). To sample *available* habitat, we selected two random compass bearings and randomly chose distances in 5-m intervals from 30 to 50 m from the center of the known *used*

sites. The end point of this transect was the center of a 20-m² habitat-sampling plot. Generally, we measured two samples of *available* habitat for every sample of *used* habitat. We measured distance to standing water for each plot as a metric of moisture availability. For cases in which we could not detect water within a reasonable distance of the plot, we entered the maximum distance we could accurately measure, which was always greater than 200 m but ranged up to 640 m. We transformed the distance to water (d , in m) to an exponential decay of the form $e^{(-d/10)}$. Thus, the influence of water diminished quickly and was essentially irrelevant at distances >20 m. Exponential decays ranged from 1 at the used site to 0 at very long distances. To maintain consistency in interpretation of coefficients (i.e., positive coefficients represent farther distances), we subtracted the exponential decay variable from 1, obtaining a distance metric that ranged from 0 at the site to 1 at very long distances.

In alpine areas, aspect can affect ambient temperature and snow melt and may influence the ptarmigan's thermal regulatory behavior. We transformed aspect as $x = -1 \cos[\theta(\pi/180)]$, where θ is the aspect measured in degrees. This transformation yielded values closer to 1 where the angle of solar incidence was higher (south-facing slopes) and values closer to -1 where it was lower. Since the importance of aspect depends on slope, we assigned aspects with slopes of <5° a neutral value of 0 (Whittington et al. 2005). The role of aspect as an effective means of thermal regulation changed through the day, so we also examined the interaction of aspect and time of day. We divided each 20-m² habitat-sampling plot into quarters with rope. We estimated percent cover of each variable for each quarter (5 m²) visually (Booth et al. 2006), then calculated percent cover for the entire 20-m² habitat plot in the lab from the ocular estimates for each quarter. Percent cover variables were arcsine-square-root transformed prior to analysis for a closer approximation of a normal distribution (Zar 1999). In instances where $|r|$ between two variables was >0.65, we removed one variable, retaining the most biologically relevant variable (Table 1). The percent shrub cover at

a site was correlated >0.65 with the number of trees at the site. Small trees were rare in the alpine habitat and occurred at approximately half the number of sites shrubs did (trees in 11% of sites, shrubs 19%). Given the difference in abundance of trees and shrubs, if White-tailed Ptarmigan are using either for cover from predators or for thermal regulation, shrubs are more accessible. Furthermore, we could estimate shrub cover accurately by eye. Accurate estimation of tree cover was more challenging because we could not view trees from above. Therefore, we based the abundance of trees at a site on the number of trees. The amount of cover (e.g., percent shrub cover) is likely more relevant to birds than is the number of trees. To compare used and available sites, we recorded data in a pairwise format and used paired logistic regression (Compton et al. 2002). Analyses were run in STATA version 10.1.

Food availability. The White-tailed Ptarmigan is a herbivore that spends much of its time foraging (25–30% of daily activity, Artiss and Martin 1995). On Vancouver Island, during brood rearing, White-tailed Ptarmigan feed primarily on the flowers of the ericaceous shrubs white mountain-heather (*Cassiope mertensiana*) and pink mountain-heather (*Phyllodoce empetrififormis*; Martin et al. 2004). They also feed regularly on the seeds of alpine grasses and sedges and the flowers of other forbs such as the partridge foot (*Luetkea pectinata*; B. Fedy, unpubl. data; Appendix A). All of these potential food sources were captured in our ocular estimates of percent cover at each site.

Predator avoidance. The risk of predation alters the habitat-selection behavior of many prey species (Fedy and Martin 2009, Hik 1995, Sih and Christensen 2001, Verdolin 2006). White-tailed Ptarmigan are prey for an array of predators, with raptors representing the primary predators of adult birds (Braun et al. 1993). Ptarmigan chicks are precocial and experience high levels of predation (~35%) during their hatch year (Hannon and Martin 2006). Sandercock et al. (2005a, b) compared the life-history strategies of the ptarmigans and found that in Colorado the White-tailed follows a survivor,

TABLE 1. Uncorrelated habitat variables quantified at each sampling plot and associated models.

Variable	Abbreviation	Description	Range	Model ^a
Aspect	aspect × time	Orientation of steepest slope angle, measured with a compass	0–360°	Th
Distance to water	d. water	Distance to nearest surface water	0–637 m	Th
Boulder cover	boulder	Percent of plot covered by bedrock or boulders >30 cm in diameter	0–100 %	Pr
Shrub cover	shrub	Percent of plot covered by woody plants >30 cm tall. Common species: <i>Tsuga mertensiana</i> , <i>Pinus contorta</i>	0–100 %	Pr, Th
Ericaceous cover	e. shrub	Percent of plot covered by ericaceous shrubs ≤30 cm tall. Common species: <i>Cassiope mertensiana</i> , <i>Phyllodoce empetrififormis</i>	0–100 %	F
Forb cover	forb	Percent of plot covered by forbs. Common species: <i>Luetkea pectinata</i> , <i>Silene acaulis</i>	0–43 %	F
Graminoid cover	gramin	Percent of plot covered by grasses and sedges. Common species: <i>Festuca occidentalis</i> , <i>Carex nardina</i>	0–55 %	F

^aF, food availability; Pr, predator avoidance; Th, thermal regulation.

or possibly bet-hedging, life-history strategy. Therefore, because adult survival plays a dominant role in the population dynamics of species with these life histories, predator avoidance could strongly influence the habitat-selection behavior of White-tailed Ptarmigan. Because of the high visibility in alpine areas, we could detect and record avian predators easily when they were flying. We noted the species and abundance of all potential predators of adults, chicks, and nests of the ptarmigan. The most abundant predators were primarily avian and included the Common Raven (*Corvus corax*), Bald Eagle (*Haliaeetus leucocephalus*), Golden Eagle (*Aquila chrysaetos*), Red-tailed Hawk (*Buteo jamaicensis*), and Northern Goshawk (*Accipiter gentilis*); other predators included wolves (*Canis lupus*) and cougars (*Felis concolor*; B. Fedy and K. Martin, unpubl. data; Martin and Elliot 1996, Martin and Commons 1997). We calculated predator abundance in terms of the number of person-hours spent surveying for birds in each region. The primary focus of the surveys was the White-tailed Ptarmigan, but we recorded all species observed. The number of person-hours spent surveying does not include hours spent capturing birds or recording habitat data. Predators were recorded only once in a location on a given day.

Thermal regulation. In the alpine zone on Vancouver Island, summer temperatures frequently reached 30 °C and higher. The evaporative efficiency of the White-tailed Ptarmigan is low while the insulative value of its feathers is high, making it poorly adapted to high ambient temperatures (Veghte and Herreid 1965, Johnson 1968). Thus it requires habitat characteristics that reduce energy demands of thermoregulation. Birds crouch in shallow puddles of water, bathe in snow, and flutter their gular skin when the ambient temperature exceeds 21 °C (Bradbury 1915, Johnson 1968). Because we collected habitat-selection data during the warmest months of the year, individual White-tailed Ptarmigan may have selected shaded areas with lower angles of solar incidence to assist with thermoregulation.

General models. To identify key habitat variables, we used an AIC approach to select the best model for each a priori hypothesis (Burnham and Anderson 2002). Previous studies of the White-tailed Ptarmigan's habitat use suggest it is a specialist in its selection of habitat, choosing moist areas of predominantly willow cover (Frederick and Gutierrez 1992, Giesen and Braun 1992, Allen and Clarke 2005, Wilson and Martin 2008). However, willow is scarce in the alpine areas of Vancouver Island, so we predicted a more generalist approach to habitat selection by this subspecies. Therefore, after selecting the best model for each hypothesis, we built general models by comparing all possible combinations of the variables identified in the top models for each hypothesis.

REGIONAL VARIATION IN POPULATION PERFORMANCE

The smaller, more isolated populations in the southern region of the island occupy smaller habitat patches, from which the

probability of extirpation may be higher (Hanski 1998), due to either low reproductive success or low survival. We predicted that population performance would be lower in the southern region of the island. We used three variables to quantify overall population performance: (1) age structure (adult, yearling), (2) sex ratio, and (3) females' reproductive success. These variables capture production of juveniles, recruitment, and potential for population-level production and combined to give an accurate indication of overall population performance.

Age structure. The survival and reproductive success of older breeding females are higher than that of younger birds (Wiebe and Martin 1998a). Therefore, populations with an age structure biased toward older birds have the potential for higher reproductive output and future population growth. We also predicted a greater proportion of older birds in the central region of the island because an age structure skewed toward older birds implies higher population performance, both as an indirect indication of survival and because the reproductive output of older birds is higher than that of younger birds. We categorized birds as either adults (>11 months old) or yearlings (9–11 months old, i.e., hatched the previous season). We combined data from all 8 years of the study; 31% of marked birds (57 of 182) were observed in >1 year, and we considered each year an independent data point for this analysis. In addition, we used a subset of individuals ($n = 142$) of known age (>11 months) to examine the effect of region on the age of known-age birds of both sexes. We analyzed the data by GLMM with a Poisson distribution and individual identity and year as random factors. We specified a compound-symmetry covariance structure that had constant variance and covariance suitable to the correlation of observations of age over years. The specification of the covariance structure resulted in the appropriate normal distribution of residuals.

Sex ratios. We also predicted different sex ratios in the two regions as another indication of population performance. In most monogamous birds, the sex ratio is male-biased (Wittenberger and Tilson 1980, Black 1996), and when populations of monogamous species decline, it typically becomes more male-biased (Hannon and Martin 1992). The White-tailed Ptarmigan is a monogamous species with low rates of extra-pair paternity (Benson 2002), and populations are generally characterized by an excess of males (Braun et al. 1993). Therefore, we predicted a sex ratio more biased toward males in the more fragmented southern region than in the central region. In surveys of Vancouver Island White-tailed Ptarmigan, the probability of encountering each sex is not equal. Females are easier than males to find during chick rearing (if they have chicks), and unmarked males are easier to locate when they are territorial during the early season. Our field work extended from May to October, so we encountered both. However, we used the same survey techniques in both the southern and central regions, so biases introduced by the techniques should be consistent in both regions, allowing for reliable

regional comparisons. We considered only breeding-age birds (yearling and older) in the analysis of sex ratios. We analyzed all frequency data with chi-squared tests.

Female reproductive success. White-tailed Ptarmigan chicks remain with the hen until they reach independence in the fall of their hatch year (~60 days of age, Hannon and Martin 2006). Chicks are capable of sustained flights at ~25 days after hatching. We determined reproductive outcome by following radio-tagged hens, considering a female successful if her young survived to 25 days by convention and because juvenile grouse experience the highest mortality during their first 2 weeks (Hannon and Martin 2006).

We used a GLMM with a Poisson distribution to examine differences in females' reproductive success (0–7 chicks per female) between the two regions. We included one observation per year per female observed between mid-July and late September. If a female observed during the period after hatching was without chicks, unresponsive to the chick-distress calls, and flocking with other adults, we assumed it was unsuccessful. The analysis included reproductive-success data from 98 individual females (southern $n = 21$, central $n = 77$) over 8 years (1995–1999, 2002–2004). Because some females were observed in multiple years, the total number of female-year observations contributing to the analysis of reproductive success was 125 (southern $n = 29$, central $n = 96$). We entered individual identity and year into the model as random factors to isolate the effect of region on female reproductive success.

We examined regional variation in reproductive success by quantifying the proportion of successful hens. In addition to providing information on female reproductive success, the percentage of successful hens can also provide indirect information regarding the level of predation in the two regions: a greater proportion of hens without young suggests greater predation pressure on either eggs or chicks. However, female reproductive success could also be influenced by other factors such as food availability.

REGIONAL VARIATION IN KEY HABITAT VARIABLES

From the models, we identified key habitat variables by examining the parameter estimates (β values) and their standard errors. We used data from the 500 sites of habitat-selection sampling to compare the distribution of these key habitat variables in the southern and central regions with a Mann–Whitney U -test.

RESULTS

FINE-SCALE HABITAT SELECTION

We recorded data on 500 plots (used $n = 176$, available $n = 324$) contributing to the habitat-selection models over 2003 ($n = 11$ individuals) and 2004 ($n = 18$ individuals; Table 2). We used the top models ($\Delta AIC_c \leq 2$) for each a priori hypothesis

TABLE 2. Fine-scale sampling of the White-tailed Ptarmigan's habitat selection on Vancouver Island. Each session was an approximately 3.5-hr observation of an individual ptarmigan. Each plot covered 20 m².

Region	Sessions	Plots		
		Used	Available	Total
Central	23	148	272	420
South	6	28	52	80
Total	29	176	324	500

(Table 3) to select the candidate variables for inclusion in the overall general models. Table 4 presents the top models ($w_i \geq 0.05$) from an AIC_c comparison of all possible combinations of the variables identified by the top models associated with each habitat-selection hypothesis. None of the key predictor

TABLE 3. Ranking of models for the three a priori hypotheses concerning the White-tailed Ptarmigan's habitat use on Vancouver Island. Variables defined in Table 1. K , number of parameters in the model; AIC_c , Akaike's information criterion adjusted for small sample size; ΔAIC_c , difference in AIC_c from the model with the lowest AIC_c ; rank, model's rank within the set; w_i = model's weight within the set.

Model	K	ΔAIC_c	Rank	w_i
Food				
e. shrub + gramin ^a	2	0.0	1	0.72
e. shrub + gramin + forb	3	1.9	2	0.28
e. shrub	1	21.4	3	<0.01
e. shrub + forb	2	22.8	4	<0.01
gramin	1	19.5	5	<0.01
gramin + forb	2	24.1	6	<0.01
forb	1	37.8	7	<0.01
Predation				
boulder ^b	1	0.0	1	0.71
boulder + shrub	2	1.8	2	0.29
shrubs	1	32.5	3	<0.01
Thermal regulation				
shrubs ^c	1	0.0	1	0.37
d. water	1	1.4	2	0.18
shrubs + d. water	2	1.4	3	0.18
aspect \times time + aspect + time	3	2.4	4	0.11
shrubs + aspect \times time + aspect + time	4	3.1	5	0.08
d. water + aspect \times time + aspect + time	4	3.3	6	0.07
shrubs + d. water + aspect \times time + aspect + time	5	6.5	7	0.01

^a $AIC_c = 321.1$

^b $AIC_c = 327.7$

^c $AIC_c = 360.2$

TABLE 4. Summary of best models in a comparison of all possible subsets of models based on the key variables identified in Table 3. Only models with a $w_i \geq 0.05$ are presented. Notation defined in Table 3.

Model	k	ΔAIC_c	Rank	w_i
boulder + e. shrub + gramin + forb + shrub + d. water ^a	6	0.0	1	0.49
boulder + e. shrub + gramin + forb + shrub	5	0.7	2	0.35
boulder + e. shrub + gramin + forb + d. water	5	3.9	3	0.07
boulder + e. shrub + gramin + forb	4	4.0	4	0.07

^a $AIC_c = 241.6$

variables had standard errors that overlapped zero, indicating they are all important and informative. Coefficients revealed positive associations with several cover variables (percent ground cover of boulders, ericaceous shrubs, graminoids, forbs, and shrubs) that indicated higher probability of use with higher percentages of those variables. A negative coefficient associated with distance to water indicated that probability of use of a site decreases with increasing distance from water; that is, the birds selected wetter areas (Table 5).

REGIONAL VARIATION IN POPULATION PERFORMANCE

Age structure. The southern region had a proportion of yearling birds higher than the central regions' (southern: 31/87 = 36% yearlings; central: 41/164 = 25% yearlings, $n = 251$, one-sided $\chi^2_1 = 3.1$, $P = 0.05$, Table 6). Although the birds in the central region tended to be older than those in the southern region, the influence of region on the age of known-age birds ≥ 1 year old was not statistically significant (range 1–5 years, $\beta = 0.14$, $SE = 0.06$, $t = 2.2$, $P = 0.16$, Table 6).

Sex ratio. In the central region, females constituted 58% of the marked population (95 females 69 males), whereas in the southern region they constituted only 37% of the marked population (32 females, 55 males; $\chi^2_1 = 10.1$, $P = 0.01$; Fig. 1).

TABLE 5. Model-averaged coefficients and standard errors for each key habitat variable. All coefficients had standard errors that did not overlap zero.

Variable	Coefficient	SE
Boulder cover	4.53	0.49
Ericaceous shrubs	3.92	0.38
Graminoids	4.10	0.93
Forbs	3.11	1.17
Distance to water	-0.94	0.12
Shrubs	1.89	0.42

TABLE 6. Age structure of White-tailed Ptarmigan captured in the southern and central portions of Vancouver Island by year.

Year	Southern			Central			Total
	Adult	Yearling	Total	Adult	Yearling	Total	
1995	7	1	8	14	2	16	24
1996	12	6	18	20	6	26	44
1997	12	2	14	35	10	45	59
1998	9	7	16	24	7	31	47
1999	8	9	17	1	—	1	18
2003	5	5	10	10	4	14	24
2004	3	1	4	19	12	31	35
Total	56	31	87	123	41	164	251

Female reproductive success. Region strongly influenced the breeding success of female White-tailed Ptarmigan, with reproductive success in the central region (mean number of chicks = 3.7 ± 0.27 per female, $n = 77$ females) of the island consistently higher than in the south (mean number of chicks = 2.0 ± 0.52 per female, $n = 21$ females, GLMM $\beta = 0.56$, $SE = 0.19$, $df = 20$, $t = 2.9$, $P = 0.01$), unsuccessful hens included. The central region also had a much higher proportion of successful hens (87%) than did the south (55%; $\chi^2_1 = 13.8$, $P < 0.001$).

REGIONAL VARIATION IN KEY HABITAT VARIABLES

We used habitat-sampling plots to analyze differences in key habitat variables between the central ($n = 420$ plots) and the south ($n = 80$ plots) regions of the island. Boulder cover in the two regions did not differ (Mann–Whitney U -test, $U = 1.1$, $P = 0.29$; Fig. 2A). Ericaceous shrub cover did differ, the southern region having the greater subshrub cover ($U = 4.1$, $P < 0.001$; Fig. 2B). Cover of graminoids was greater in the central region than in the south ($U = 2.1$, $P = 0.04$; Fig. 2C).

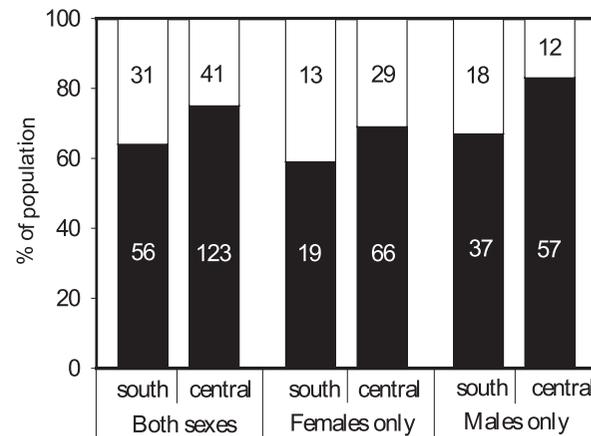


FIGURE 1. Comparison of the age categories of the White-tailed Ptarmigan in the southern and central regions of Vancouver Island. Black bars, adults ≥ 2 years old; white bars, yearlings. The numbers inside the bars represent the respective sample sizes.

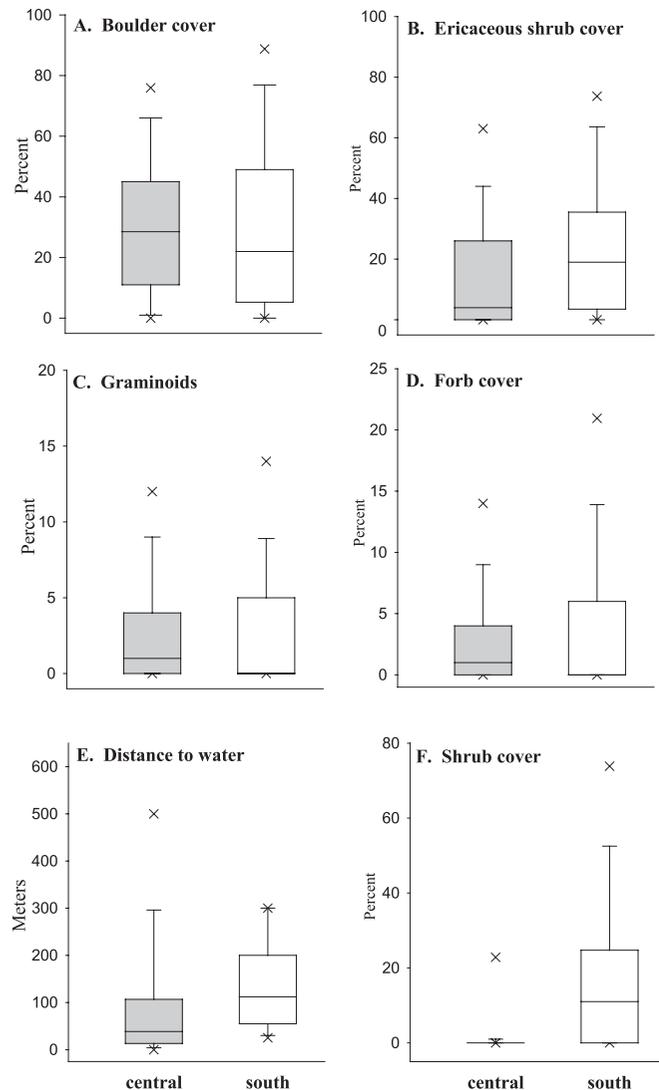


FIGURE 2. Box plots comparing regional variation in the distribution of habitat variables important to the White-tailed Ptarmigan on Vancouver Island. The 5th and 95th percentiles are denoted by \times .

Forb cover did not differ ($U = 0.2$, $P = 0.89$; Fig. 2D). Plots in the central area were consistently closer to water than were the southern plots ($U = -6.0$, $P < 0.001$, Fig. 2E). Greater shrub cover in the southern region likely a result of the lower elevation of the alpine areas there ($U = -10.8$, $P < 0.001$, Fig. 2F).

PREDATOR ABUNDANCE

The abundance of predators (raptors, ravens, bears, wolves) in the southern and central regions of the island differed only slightly. In the southern region, we recorded an average of 1.7 predators per 10-hr day [(307 predator detections/1755 person-hours) \times 10 hr], in the central region 1.4 predators per 10-hr day [(273/1968) \times 10 hr]. As noted above, the proportion of successful hens in the two regions differed significantly, being much higher in the central region.

DISCUSSION

White-tailed Ptarmigan selected for multiple fine-scale habitat components associated with food availability, predator avoidance, and thermal regulation. Regional variation in population performance was in the direction predicted from metapopulation theory, with the southern region of more fragmented habitat having younger birds, a lower ratio of females, and lower annual reproductive success per female. The distribution of several key habitat variables associated with food availability differed regionally, but not always in the predicted direction. Therefore, the results were equivocal regarding the influence of food availability on variation in population performance. However, the distance to standing water and predation differed in the predicted directions and may play a role in regional variation in population performance. Variables carried forward from each of the a priori hypotheses were retained in the final top models (Table 4). The combination of multiple covariates representing different drivers of habitat selection suggested a gradient in the White-tailed Ptarmigan's behavior with the Vancouver Island subspecies having a more generalist approach to habitat use than mainland populations that specialize on willow (Choate 1963, Weeden 1967, May and Braun 1972, Herzog 1977, 1980, Frederick and Gutierrez 1992, Giesen and Braun 1992, Allen and Clarke 2005).

IDENTIFICATION OF KEY HABITAT VARIABLES

Our fine-scale resource-selection data were collected during brood rearing, an important period for the survival and training of juvenile birds (Allen and Clarke 2005, Hannon and Martin 2006). The avoidance of predators by both adults and juveniles was reflected in selection for areas with more boulder cover and, perhaps, shrub cover. In addition to providing cover from predators, boulders and shrubs could also provide shade, aiding the birds' thermoregulatory demands.

White-tailed Ptarmigan selected sites with greater cover of preferred food items including ericaceous shrubs, graminoids, and forbs. On Vancouver Island, pink and white mountain heather begin to bloom at the end of June, and their flowers are available through August (B. Fedy, unpubl. data). Moisture levels may have influenced the production of inflorescences on the ericaceous shrubs, but we could not test for differences between regions in the abundance of flowers. The fruits of other subshrubs such as crowberry (*Empetrum nigrum*) and bear berry (*Arctostaphylos uva-ursi*) may replace the heather as a food source later in the season. Birds may specialize on ericaceous shrubs throughout the year, but our sampling was restricted to late summer. On Vancouver Island, however, ptarmigan likely use several plant species, in contrast to areas where willow is abundant.

Wilson and Martin (2008) demonstrated that the habitats of breeding White-tailed and Rock Ptarmigan are differentiated primarily by elevation, slope, and the ground cover of

lichens and graminoids. At their study site, White-tailed Ptarmigan selected drier habitats dominated by lichens, and Rock Ptarmigan occupied wetter areas with more graminoid cover. In our study, White-tailed Ptarmigan used wetter sites with more graminoid cover. In the Yukon the larger Rock Ptarmigan may exclude the White-tailed from the preferred wetter sites. Our results were consistent with observations of Wilson and Martin (2008) that the White-tailed Ptarmigan may have a broader niche where it is the only species of grouse (Braun et al. 1993, Wiebe and Martin 1998b).

REGIONAL VARIATION IN POPULATION PERFORMANCE

Population performance, based on greater proportion of younger females, more male-biased sex ratio, and lower female reproductive success, was lower in the southern region than at the central sites. Female White-tailed Ptarmigan have strong age-dependent differences (Sandercock et al. 2005a). First-year birds have significantly higher annual mortality, have poorer body condition in spring, lay later and smaller clutches, and reneest less than older birds (Wiebe and Martin 1998a, Sandercock et al. 2005a). Therefore, the difference between the southern and the central regions in proportion of juvenile birds likely represented a biologically meaningful pattern. Furthermore, our analysis of known-age birds also showed a trend in the predicted direction, toward older birds in the central region of the island. The much lower proportion of females in the south region provided further indication of that population's lower performance. The difference in age structure could be an important influence on the reproductive success of females and may contribute to the difference in reproductive success between the two regions.

The lower population performance in the southern region is consistent with predictions from metapopulation theory (Hanski and Simberloff 1997). On Vancouver Island, alpine areas represent habitat patches suitable for the White-tailed Ptarmigan surrounded by a matrix of unsuitable, low-elevation habitat. Most metapopulation studies report that a coarse-scale measurement of patch area and the degree of isolation between patches is sufficient to predict patch occupancy (Thomas and Jones 1993, Hanski 1998, Moilanen and Hanski 1998). Alpine areas in the south of the island are more isolated and offer less habitat than the central region. However, habitat quality may also influence metapopulation dynamics (Moilanen and Hanski 1998).

FINE-SCALE HABITAT VARIABLES AND REGIONAL VARIATION

Food and distance to standing water may influence population performance. The brood-rearing period is an important stage for the reproductive success of White-tailed Ptarmigan (Hannon and Martin 2006). A greater availability of ericaceous shrubs in the southern region suggested a greater availability of this key food source in this region; however, this finding was counter to the prediction that food availability during brood rearing is

important to population performance. Regional variation in secondary food sources (graminoids and forbs) was equivocal regarding the influence of food availability on population performance, so food availability may not be a limiting factor at this life-history stage. However, the greater experience of the central birds (higher proportion of adults) in finding quality forage may offset any potential regional variation in population performance due to food availability. Birds used wetter sites, and the south was drier than the central region. Although White-tailed Ptarmigan seldom get moisture directly from open water, they tend to prefer wetter sites perhaps because of greater availability of insects or thermal regulatory needs (Herzog 1977, Frederick and Gutierrez 1992, Allen and Clarke 2005). Thus distance to standing water (as a metric of moisture availability) correlated with population performance in the predicted direction. We return to our original question: can we scale up from individual-level choices and fine-scale habitat features to population-level processes? As with many questions in ecology, the answer is not simple for White-tailed Ptarmigan on Vancouver Island. Between the regions, several (but not all) of the preferred habitat components differed in the predicted direction. We suggest that coarse-scale components (e.g., patch area and isolation) and fine-scale components (e.g., food availability, cover) likely interact to influence regional variation in population performance in the White-tailed Ptarmigan. As noted above, the species' habitat-selection behavior on Vancouver Island is somewhat different from that elsewhere in its range. Our sampling captured the majority of its distribution on Vancouver Island, but we recommend caution if our conclusions are extrapolated to other populations.

CLIMATE-CHANGE IMPLICATIONS

The Pacific Northwest, including Vancouver Island, is experiencing significant increases in temperature as a result of global climate change (Service 2004, Wang et al. 2006, IPCC 2007). For Vancouver Island, an upward elevational shift in biogeoclimatic zones and a significant decrease of alpine habitat are predicted (Hebda 1998, Wang et al. 2006). The rising tide of low-elevation communities and treelines will likely result in smaller patches of the White-tailed Ptarmigan's habitat, greater distances between populations, and increased interspecific competition. Essentially, the central area may progress, structurally and functionally, to the patterns current in the southern area. Given the findings of our study, greater isolation and smaller patches may result in decreased population performance that could threaten the persistence of this endemic subspecies of White-tailed Ptarmigan.

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APPENDIX. Food items taken by 15 adult White-tailed Ptarmigan observed for over 20 hr of observation in continuous 15-min increments. Plant names follow Pojar and MacKinnon (1994).

Botanical name	Common name	Plant part taken
<i>Cassiope mertensiana</i>	White mountain heather	flowers
<i>Phyllodoce empetriformis</i>	Pink mountain heather	flowers
<i>Phyllodoce glanduliflora</i>	Yellow mountain heather	flowers
<i>Empetrum nigrum</i>	Crowberry	fruit
<i>Luetkea pectinata</i>	Partridge foot	flowers
<i>Lloydia serotina</i>	Alp lily	leaves
<i>Vaccinium</i> spp.	Blueberries and huckleberries	fruit/leaves
<i>Salix arctica</i>	Arctic willow	leaves
<i>Saxifraga tolmiei</i>	Tolmie's saxifrage	flowers
<i>Sedum divergens</i>	Spreading stonecrop	flowers
graminoid spp.	Grasses	seeds
<i>Carex</i> spp.	Sedges	seeds
	Insects	