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Breeding habitat selection of sympatric White-tailed, Rock and Willow Ptarmigan in the southern Yukon Territory, Canada

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Abstract We examined breeding habitat selection at two scales for White-tailed (*Lagopus leucura*), Rock (*L. muta*), and Willow Ptarmigan (*L. lagopus*) at an alpine site in the Ruby Range Mountains of the Yukon Territory, Canada. To infer species-specific preferences, we used logistic regression and AIC model selection to compare nest habitat of White-tailed ($n = 43$) and Rock Ptarmigan ($n = 58$). Only descriptive statistics were used for Willow Ptarmigan ($n = 8$ nests) because of smaller sample sizes. Modeling results indicate elevation, slope, and the ground cover of graminoids and lichens were the main variables separating White-tailed and Rock Ptarmigan breeding habitat. Average estimates for elevation and slope around nest sites of each species followed a pattern of White-tailed Ptarmigan (1,827 m, 30°) > Rock Ptarmigan (1,728 m, 18°) > Willow Ptarmigan (1,512 m, 6°). White-tailed Ptarmigan tended to select drier habitats dominated by lichens, rock and dwarf shrubs, while Rock Ptarmigan were more common in meadows with graminoids and scattered woody shrubs. Willow Ptarmigan nested in areas with dense, woody shrubs. The three species display inter- and intraspecific territoriality, and while species-specific habitat preferences allow co-existence, the niche width of each is likely narrowed by the presence of congeners, particularly for White-tailed and Rock Ptarmigan. Within territories, all three species selected nest sites with more lateral cover than expected at random (24–50%). White-tailed and Rock Ptarmigan did not select specific cover types (vegetation or rock) for nest sites within territories, while most Willow Ptarmigan nests were located in patches of scrub birch (*Betula glandulosa*).

Keywords Alpine tundra · Interspecific competition · Lagopus · Nest habitat · Ptarmigan

Introduction

Selection of avian breeding habitat occurs in a hierarchical fashion (Wiens et al. 1987; Orians and Wittenberger 1991). At landscape levels, settlement may be largely determined by the availability and configuration of suitable habitat features, while at finer scales, habitat selection may be further influenced by other ecological factors (Cody and Walter 1976; Fontaine and Martin 2006). Interspecific competition among related species (e.g., congeners) can be a particularly important factor affecting the range of breeding habitat occupied (Garcia et al. 1983; Kumstátová et al. 2004). In areas where congeneric species are sympatric, species-specific breeding habitat preferences may reduce the extent to which competition limits habitat selection (e.g., Rolando and Palestrini 1989). It is in cases where congeric species display interspecific territoriality and have similar habitat preferences that competition should have the greatest influence on settlement patterns (Alatalo et al. 1985; Bourski and Forstmeier 2000). At the finest scale, breeding females must also select a nest site

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within territories, and individuals often select locations that offer protection from predators and climatic factors (Martin 1992; Etterson et al. 2007). Knowledge of the factors affecting habitat selection at multiple scales can help our understanding of the fitness and demographic implications of habitat selection and aid conservation decisions (Caughley 1994; Jones 2001).

We examined breeding habitat selection of White-tailed (*Lagopus leucura* formerly *leucurus*; American Ornithologists' Union 2006), Rock (*L. muta*, formerly *mutus*; American Ornithologists' Union 2006) and Willow Ptarmigan (*L. lagopus*) at a site where all three co-exist in the southern Yukon Territory, Canada. Ptarmigan are monogamous, ground-nesting grouse that inhabit tundra environments throughout their range. Nesting typically begins soon after snowmelt and females produce a single brood of precocial young annually, but will renest following nest failure. White-tailed Ptarmigan are the smallest of the three, followed by Rock and Willow Ptarmigan (Braun et al. 1993; Hannon et al. 1998; Holder and Montgomerie 2008). Previous studies have examined habitat selection where these species exist individually, but there are almost no detailed studies on how all three segregate in geographic locations where they co-occur (but see Weeden 1959). White-tailed Ptarmigan are restricted to western North America from New Mexico through Alaska where they inhabit alpine tundra (Frederick and Gutierrez 1992; Braun et al. 1993). Rock and Willow Ptarmigan have circumpolar distributions; the former typically breeds in sparse alpine and arctic tundra (Holder and Montgomerie 1993; Favaron 2006), while the latter selects shrubby subalpine and subarctic tundra (Schieck and Hannon 1993; Hannon et al. 1998; Campbell et al. 2002). The three species overlap from northern British Columbia through south-central Alaska where competition may limit the range of habitat used by each. Willow Ptarmigan are socially dominant over Rock Ptarmigan in areas of sympatry (Moss 1972), but the latter avoid dense shrubs during breeding and this may lower competition. Rock and White-tailed Ptarmigan select habitats with similar structure, providing the potential for increased competition for breeding territories where they co-exist.

To investigate the extent to which these three species segregate in selection of breeding habitat, we first compared topographic and vegetation features among nest sites of each as an indication of territory level habitat differences across the study area. Interspecific habitat selection is more likely related to initial settlement and competition among males, but as we show the habitat around nests within territories is a reliable measure of differences between species. To better understand what might lead to interspecific patterns, we also conducted a restricted analysis between White-tailed and Rock Ptarmigan across a

narrow elevational zone where they are present in equal abundance. We then considered how females of each species select nest sites within territories. When compared against environmental conditions, intraspecific comparisons of nest and random sites can provide insight into why females select particular sites (Wiebe and Martin 1998).

Methods

Study area

The study was conducted in the Ruby Range Mountains of the Kluane region, Yukon Territory (61°13′N, 138°16′W) from 2004 through 2006. Mean daily temperatures at the site averaged approximately 8°C during the peak breeding period (mid-May to end-July) and −15°C in mid-winter (December–February). The Kluane region is classified as semi-arid and precipitation is typically less than 30 cm per year, most of which falls as rain during the summer months (Krebs and Boonstra 2001). The study site consisted of 10 km² of alpine and subalpine habitat (1,400–2,200 m elevation). The upper subalpine zone at approximately 1,400–1,500 m contained large patches of woody shrubs [primarily tealeaf willow (*Salix pulchra*), grayleaf willow (*S. glauca*) and scrub birch (*Betula glandulosa*)] interspersed with lower vegetation, (e.g., sedges (*Carex* spp.)) and small wetlands. The zone from 1,500 to 1,750 m was a transition from subalpine to high alpine and consisted of meadows of sedges, grasses and rushes, mixed with smaller patches of woody shrubs, rock outcrops and dwarf shrubs. Higher elevation habitats above 1,750 m have few woody shrubs and are dominated by rocky areas mixed with low vegetation, mostly dwarf shrubs and lichens. Common dwarf shrubs at the study site included white mountain avens (*Dryas octopetala*), net-leaved willow (*Salix reticulata*), polar willow (*S. polaris*) and arctic willow (*S. arctica*). These dwarf shrubs were typically less than 3 cm in height with most of their woody base underground. Smaller patches of four-angled mountain heather (*Cassiope tetragona*) and moss were interspersed throughout the site. Over the 3 years, densities of Rock and White-tailed Ptarmigan, respectively, ranged from approximately 4–5 and 2–3 pairs/km². Willow Ptarmigan were only located on approximately 10% of the study area at about 3 pairs/km².

Field methods and habitat sampling

Fieldwork was conducted from early May through July of each year. Prior to breeding, individuals of both sexes were caught using ground nets or noose poles, and were marked with an aluminum band on one leg and a numbered plastic color band on the other. Females were fit with a 4- or 7-g

radio-transmitter (Holohil, Carp, ON) to facilitate nest finding. We located females every 1–3 days until the nest was located, and monitored it to determine nest fate. Ptarmigan leave the nest immediately after hatch, and nest habitat was measured within 7 days of hatch for successful nests or the expected date of hatch for failed nests. For each nest, we also measured habitat at a random site within the territory, which was selected by spinning a compass to determine a distance and angle from the nest. For the random site, we made a depression similar to the shallow scrape females construct for their nest prior to measurement.

Nest habitat was measured on a 10-m diameter plot around each nest. We first measured topographic features including elevation (m), slope aspect (from 0° to 360°) and angle of the slope (degrees). We also calculated distance to shrubs <1 m in height, >1 m in height, rock (continuous cover >1 m^2) and standing water. To measure overhead and lateral cover, we placed a cloth the size of a sitting female in the scrape. Overhead cover was estimated as the percent of the cloth obstructed when looking down on the nest from 1 m, and lateral cover as the average percent of the cloth concealed when looking at the nest from each of the four cardinal directions at a height of 0.3 m above the ground and 1 m from the nest. We chose lateral cover as an index rather than vegetation height because in tundra, rock and natural undulations also provide cover. For all sites containing woody shrubs within 1 m of the plot center, we measured stem density as the number of stems less than or greater than 2.5 cm in diameter at a height of 10 cm. For plots with woody shrubs, we measured a random sample of the shrubs to estimate mean shrub height.

Percent cover within the plot was measured for water, rock, bare ground, moss, heather, lichens (not included if on rock), sedges, grasses, rushes, woody shrubs (minimum height ≥15 cm), dwarf shrubs (maximum height <15 cm) and forbs. For our analyses, grasses (Poaceae), sedges (Cyperaceae) and rushes (Juncaceae) were collectively termed graminoids. Sedges are the most common graminoid with several species of the *Carex* genus present at the site. Percent cover was estimated as if looking down on the plot and refers to the top layer. Thus, where woody shrubs were present, the ground layer composition immediately under the shrubs would not be included. We identified lichen, heather, dwarf shrubs, woody shrubs and forbs to genus or species where possible. It was difficult to identify graminoids and mosses to genus or species across the entire plot and therefore we only identified them to functional groups.

Statistical analyses

We used standard logistic regression under a model-selection framework to compare breeding habitat of White-tailed and Rock Ptarmigan (Hosmer and Lemeshow 2000; Burnham and Anderson 2002). Given the smaller sample size, we only examined habitat selection of Willow Ptarmigan with descriptive statistics. We only used the initial nesting attempt for a female in a particular year due to confounding effects of seasonal change in vegetation on later renest attempts. Because nest site selection is restricted to areas within the territory, we only used multiple attempts for females between years if they switched territories. This was the case for six Rock Ptarmigan and four White-tailed Ptarmigan. Separate analyses without these multiple attempts produced the same results and, therefore, we used the larger data set for interpretation. For interspecific comparisons, we modeled White-tailed Ptarmigan nests as a "success" (1) and Rock Ptarmigan as a "failure" (0). Positive and negative coefficients for a variable indicate association with White-tailed or Rock Ptarmigan breeding sites, respectively.

An assumption of standard logistic regression is that any habitat within the study area is available, clearly not the case for a territorial species where the nest site is limited to habitat within the territory (Jones 2001). Thus, for intraspecific comparisons of nest versus random sites, we used paired logistic regression (Compton et al. 2002). With this method, the response variable is a vector of 1's and is regressed on a matrix of predictor variables measured as the case (nest)—the control (random site). An intercept term is excluded from the model. A positive coefficient in this case would suggest a particular variable tends to be associated with the nest site.

For analyses, we also report the odds ratio (OR) for a variable, which gives the odds of an event occurring in one group relative to the odds in the other group. For continuous predictor variables the odds ratio is estimated as $OR = \exp(c\beta_i)$, where c represents a meaningful change in the predictor variable (Hosmer and Lemeshow 2000). Global models were tested for goodness of fit using a modified version of the Hosmer–Lemeshow GOF test (Hosmer et al. 1997). All tests were performed using the R statistical language and environment (R Development Core Team 2006).

Selection of candidate models

Our aim was to identify models that separate key topographic and habitat features, and to accomplish this, we used a forward entry procedure. We first added elevation, slope and aspect. To the top models containing topographic features, we added the six cover variables: graminoids, rock, dwarf shrubs, woody shrubs, heather and lichens. An intercept only model was also included in standard logistic regression analyses, which if supported would indicate none of the variables were influential in

predicting habitat selection. For each analysis, we examined correlation coefficients among variables across plots and if r was >0.60, we only included one member of the pair in a particular model. We did not include forbs, shrub height, stem density or overhead cover in the models because either their abundance varied seasonally (e.g., forbs) or the majority of plots had zero entries. For nest–random site analyses, we used the results of interspecific comparisons to construct candidate models believed to represent the range of available cover types on the territories of each species, as well as lateral cover. Akaike's information criterion for small samples (AIC$_c$; Burnham and Anderson 2002) was used for model selection, and we used the ΔAIC$_c$ and Akaike weights to infer support for different models. Because there was no evidence of lack of fit or overdispersion, we chose AIC$_c$ rather than QAIC$_c$. Coefficients were determined using model averaging.

Results

Interspecific nest site selection

For regression analyses, we compared 23 candidate models using 43 White-tailed Ptarmigan nests from 39 females and 58 Rock Ptarmigan nests from 52 females. All top models contained elevation (combined $w_i = 1$), slope (combined $w_i = 1$), and percent cover of graminoids (combined $w_i = 0.86$; Table 1a). The addition of lichens also improved model support but to a lesser extent (combined $w_i = 0.79$). The coefficients and odds ratio estimates indicated that White-tailed Ptarmigan breeding sites tended to be at higher elevations, steeper slopes and amidst greater lichen cover, while Rock Ptarmigan preferred lower elevations with higher graminoid cover (Table 2; Fig. 1a, b). Rock cover was also higher on White-tailed Ptarmigan territories (Table 3), but because of negative correlations between graminoid and rock ($r = -0.541$), there was less support for models that included both. Rock Ptarmigan territories tended to have greater woody shrub cover, but this variable only led to a slight improvement in log-likelihood. Both species more often selected sites on the northeastern slopes of the valley, which have a southwestern aspect, although there was variability (White-tailed Ptarmigan $\bar{x} = 168°$, angular deviation $= 100.7°$; Rock Ptarmigan $\bar{x} = 199°$, angular deviation $= 85.8°$). Willow Ptarmigan were most common in subalpine habitat at lower elevations and on flatter slopes than White-tailed or Rock Ptarmigan (Table 3). Ground cover on Willow Ptarmigan territories was dominated by woody shrubs mixed with open patches of graminoids, dwarf shrubs, heather and small wetlands. Woody shrub cover on these territories contained taller *Salix* spp. (willow) with an open understory and dense patches of low *Betula glandulosa* (scrub birch).

Change in some habitat variables is correlated with elevation, and to examine whether preferences for slope and ground cover were consistent across elevations, we conducted a second analysis using White-tailed and Rock Ptarmigan nests within the 1,725–1,825 m elevational zone where the two species frequently overlap (there was

Table 1 Model selection results for nest habitat comparisons of Rock (*Lagopus muta*) and White-tailed Ptarmigan (*L. leucura*) across (a) the entire study site and (b) the 1,725–1,825 m elevational range, in the southern Yukon Territory, 2004–2006

Model	k	Log$_e$(L)	AIC$_c$	ΔAIC$_c$	w_i
(a) Entire study site					
Elev + Slope + Gramin + Lichen	5	−33.89	78.39	0.00	0.31
Elev + Slope + Gramin + Heather + Lichen	6	−32.80	78.46	0.07	0.30
Elev + Slope + Gramin	4	−36.04	80.49	2.10	0.11
Elev + Slope + Rock + Lichen	5	−35.14	80.90	2.51	0.09
Elev + Slope + Gramin + Wshrub	5	−35.65	81.91	3.52	0.05
Intercept	1	−68.89	139.82	61.43	0.00
(b) 1,725–1,825 m elevational range					
Slope + Rock	3	−18.82	44.26	0.00	0.35
Slope + Gramin	3	−18.93	44.48	0.22	0.31
Slope + Gramin + Rock	4	−18.10	45.25	1.00	0.21
Slope	2	−21.41	47.12	2.87	0.08
Intercept	1	−29.70	61.50	17.24	0.00

k the number of parameters, *Log$_e$(L)* the log-likelihood, *AIC$_c$* Akaike's Information Criterion for small samples, *ΔAIC$_c$* the scaled AIC$_c$ relative to the top model, *w_i* the Akaike weights, *Elev* elevation, *Gramin* % graminoid cover, *Wshrub* % woody shrub cover

For (a) and (b), we only show models with $w_i > 0.05$, but also include an intercept only (null) model as a control

Table 2 Model averaged coefficients and odds ratios (with 95% CI) from interspecific nest habitat comparisons (Table 1a) in the southern Yukon Territory, Canada, 2004–2006

Variable	Coefficient with 95% CI	Odds ratio (OR)	95% CI for OR
Elevation	0.011 (0.003, 0.019)	1.316 (25 m)	1.120 to 1.512
Slope	0.162 (0.073, 0.250)	1.382 (2 deg)	1.205 to 1.559
Graminoids	−0.118 (−0.197, −0.038)	0.702 (3%)	0.461 to 0.942
Lichens	0.098 (0.004, 0.192)	1.103 (1%)	0.927 to 1.280

For logistic regression, we modeled White-tailed Ptarmigan nests as a "success" (1) and Rock Ptarmigan nests as a "failure" (0)
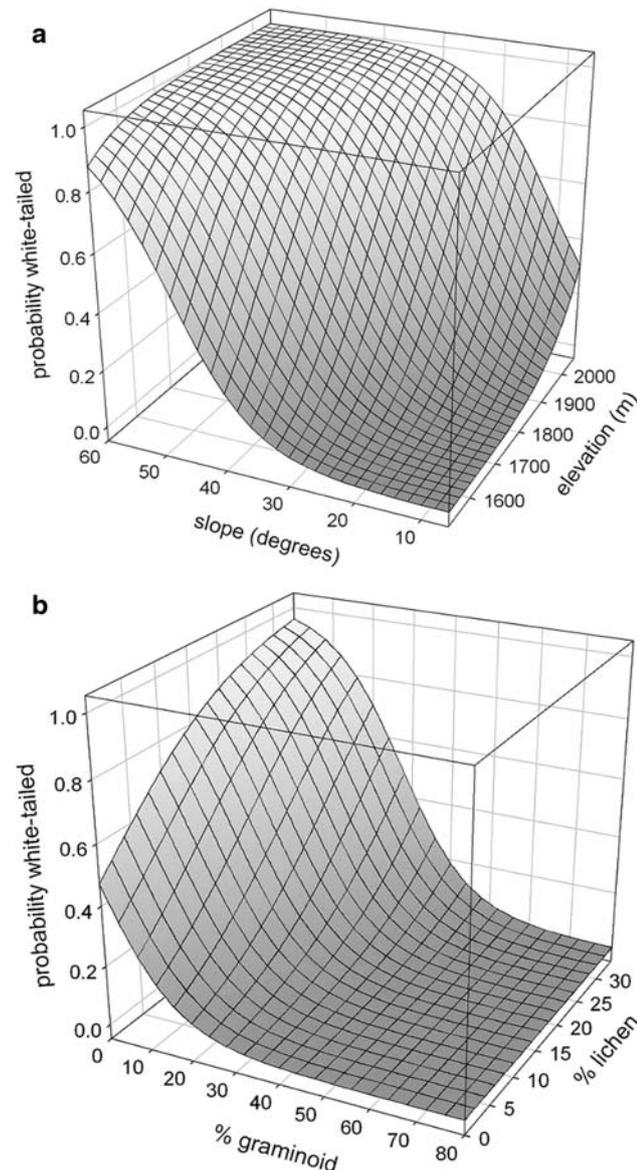

Fig. 1 Surface area plot showing the probability that a nest site would be that of a White-tailed Ptarmigan rather than a Rock Ptarmigan as a function of **a** *elevation* and *slope*, **b** *graminoids* and *lichens*. Probabilities were generated from the model averaged estimates in Table 3 and based on a sample of nests for 44 White-tailed Ptarmigan and 58 Rock Ptarmigan

not a clear zone of overlap between either of these species and Willow Ptarmigan). Within this 100-m zone there were 22 White-tailed Ptarmigan and 20 Rock Ptarmigan nests with a mean elevation of 1,778 m for the former and 1,759 m for the latter. We compared 11 models and found that slope, rock and graminoids were the best predictors of differences within this range (Table 1b). Addition of graminoid and rock together did not enhance model support, suggesting these two variables explain similar variation ($r = -0.56$ for rock and graminoids in this analysis). On average, White-tailed Ptarmigan within this zone nested on steeper slopes [$\beta_{slope} = 0.146$ (95% CI: 0.032, 0.260)] and with greater rock [$\beta_{rock} = 0.041$ (-0.006, 0.089)] and lower graminoid cover [$\beta_{gramin} = -0.085$ (-0.189, 0.019)]. There was no evidence that cover of woody shrubs, dwarf shrubs, lichens or heather differed among the two within this zone. Overall, these patterns suggest that White-tailed Ptarmigan consistently select steeper slopes and the two maintain ground cover preferences even within the same elevational zone.

Intraspecific nest site selection

To examine White-tailed Ptarmigan nest site selection within territories, we used 35 nest–random site pairs and 12 candidate models. Females selected areas with higher lateral cover, on average 30% greater than random sites (Tables 4, 5). The estimate for lateral cover was 0.082 (95% CI: 0.027, 0.139) and the odds ratio with a 5% change was 1.51 (1.23, 1.80). The inclusion of other habitat variables led to little improvement in model support. For Rock Ptarmigan, we used 53 nest–random site pairs and compared 14 models. As with White-tailed Ptarmigan, only lateral cover appeared to differ between nest and random sites, with nest sites having on average 24% greater lateral cover than random sites (Tables 4, 5). The estimate for lateral cover was 0.076 (95% CI: 0.036, 0.115) and the associated odds ratio with a 5% change was 1.46 (1.26, 1.66). Willow Ptarmigan nest sites had on average 50% greater lateral cover than random sites. They also selected sites with higher stem density, but a lower shrub height, which was largely due to a preference for nesting in dense scrub birch (*Betula glandulosa*), rather than taller and more open willows (*Salix* spp.).

Table 3 Nest site characteristics of Rock, White-tailed and Willow Ptarmigan in the Ruby Range Mountains of the Southern Yukon Territory, 2004–2006

Variable	Species								
	White-tailed Ptarmigan ($n = 44$)			Rock Ptarmigan ($n = 58$)			Willow Ptarmigan ($n = 7$)		
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Elevation (m)	1,826.9	106.0	1,585–2,052	1,715.3	82.44	1,579–1,922	1,512.0	117.0	1,413–1,647
Slope (deg)	29.8	11.4	10–63	17.8	8.6	3–44	6.0	4.9	2–16
Dist woody shrub (m)	72.8	88.0	0–300	24.3	60.2	0–301	0.01	0.005	0–0.02
% nests with shrubs within 1 m	19			34			100		
Mean # stems within 1 m[a]	15.1	11.7	1–34	51.0	33.8	1–145	113.4	43.1	45–180
Mean shrub height (m)[b]	0.29	0.16	0.12–0.58	0.36	0.13	0.19–0.70	0.42	0.11	0.25–0.55
Rock[c] (%)	34.2	24.0	0–83	10.8	14.4	0–63	0.36	0.95	0–3
Graminoids (%)	12.7	7.6	3–40	25.1	13.2	4–68	6.8	4.1	3–13
Woody shrubs (%)	1.5	3.7	0–16	8.1	13.9	0–63	74.7	17.2	42–90
Dwarf shrubs (%)	23.3	17.4	3–61	20.2	14.7	1–60	3.4	2.6	1–8
Lichens (%)	12.9	9.6	1–36	8.7	7.1	0–40	2.6	1.8	0–6
Heather (%)	5.6	10.1	0–37	7.9	12.2	0–41	0.6	1.5	0–4
Forbs (%)	4.1	2.4	1–12	6.4	4.3	0–22	3.4	2.2	1–8

[a] Woody shrub cover within 1 m

[b] Based on woody shrubs

[c] Cover (%) for all types determined from a 5-m radius plot centered at the nest

Table 4 Model results for nest versus random site comparisons for White-tailed and Rock Ptarmigan in the southern Yukon Territory, 2004–2006

Model	K	$\text{Log}_e(L)$	AIC_c	ΔAIC_c	w_i
White-tailed Ptarmigan					
Lateral	1	−10.94	24.00	0.00	0.26
Lateral + lichen	2	−9.89	24.16	0.15	0.24
Lateral + gramin	2	−10.27	24.92	0.91	0.16
Lateral + dshrub	2	−10.39	25.16	1.15	0.15
Lateral + heather	2	−10.72	25.82	1.81	0.10
Rock Ptarmigan					
Lateral	1	−20.01	42.10	0	0.26
Lateral + heather	2	−19.27	42.78	0.68	0.19
Lateral + wshrub	2	−19.46	43.15	1.05	0.16
Lateral + gramin	2	−19.80	43.84	1.74	0.11
Lateral + lichens	2	−19.89	44.02	1.92	0.10

3.70

Most variables had little influence on the log-likelihood and so we only show the models within 2AIC$_c$ units of the top model. Variable names are as for Table 1. Matched pair logistic regression was used for nest–random comparisons and does not include an intercept

Lateral % lateral cover

Table 5 Habitat differences between nest and random sites (measured as value at the nest site—value at the random site) for White-tailed, Rock and Willow Ptarmigan in the southern Yukon Territory, 2004–2006

Variable	White-tailed Ptarmigan ($n = 35$)	Rock Ptarmigan ($n = 53$)	Willow Ptarmigan ($n = 7$)
Overhead cover	12.80 ± 5.14	9.43 + 2.58	35.14 ± 11.66
Lateral cover	29.80 ± 4.48	24.15 + 3.43	49.68 ± 9.49
Dist shrub	−7.30 ± 15.34	0.74 ± 2.84	−0.76 ± 0.31
Rock	9.50 ± 4.80	0.09 ± 2.83	−0.93 ± 0.66
Graminoid	−4.20 ± 2.74	−1.98 + 2.97	−35.00 ± 7.99
Woody shrub	−3.70 ± 2.32	2.97 + 2.13	46.57 ± 8.54
Dwarf shrub	0.30 ± 3.68	−3.79 ± 2.29	−5.86 ± 3.34
Lichens	1.70 ± 1.40	−0.31 + 1.13	0.39 ± 1.53
Heather	1.20 ± 2.22	1.30 + 2.10	0.43 ± 0.61
Mean woody shrub ht[a]			−0.36 ± 0.17
Mean stems within 1 m[a]			97.57 ± 11.20

Values indicate mean difference with standard error in brackets. *n* the number of nest–random site pairs

[a] Woody shrubs were rarely present at both nest and random sites of Rock and White-tailed Ptarmigan, thus we only present values on shrub height and stem density for Willow Ptarmigan

Discussion

Interspecific nest site selection

Selection of habitat at the territory level is likely the result of initial settlement and competition among males who establish territories in late April before the arrival of females. Although our plots were centered around nest sites, random selection of a site within the territory allowed us to infer territory-level habitat features based on those plots

(but see below for Willow Ptarmigan). Based on modeling and descriptive statistics, habitat segregation was most evident by elevation, slope and ground cover. White-tailed Ptarmigan typically bred on steeper slopes in high alpine habitat with a mixed cover of rock and low vegetation (e.g., lichen, dwarf shrubs). Rock Ptarmigan territories were more often in lower alpine meadows at intermediate elevations, with a ground cover of graminoids interspersed with rock, woody shrubs and heather. Territories of the two species often adjoined in areas where rocky talus lines bisected sedge meadows. Willow Ptarmigan bred in upper subalpine habitat at the lowest elevations where the ground cover was dominated by woody shrubs. Willow Ptarmigan females tended to select nest sites in dense scrub birch, potentially biasing territory level inference. In general, Willow Ptarmigan territories have an approximately equal mix of scrub birch, taller and more open willows, and open meadows.

At elevations of approximately 1,725–1,825 m, White-tailed and Rock Ptarmigan overlapped with equal abundance. Yet patterns of selection by slope and ground cover in this zone were similar to those for the entire study site, suggesting the two maintain their habitat preferences even in close proximity to one another. Species-specific preferences for different micro-habitats would allow overlap in areas where both features are present. In Italy, where Great Reed (*Acrocephalus arundinaceus*) and Marsh Warblers (*A. palustris*) are sympatric, the former defends territories against the latter, but the two have different habitat preferences that reduce competition (Rolando and Palestrini 1989). Sympatric co-existence via habitat segregation was also observed between Tree (*Anthus trivialis*) and Meadow Pipits (*A. pratensis*) in the Czech Republic (Kumstátová et al. 2004).

Segregation between Rock and White-tailed Ptarmigan might be enhanced by interspecific territoriality as observed previously for other sympatric avian congeners (Cody and Walter 1976; Garcia 1983; Rolando and Palestrini 1989). Because our studies were observational we are uncertain as to the extent to which either species would expand their niche width in the absence of the other. Males of the two species were aggressive to one another during the pre-breeding period with frequent chases following territory intrusion. Because Rock Ptarmigan males are highly mobile during pre-breeding (due to their flight displays), it was more common for White-tailed Ptarmigan males to chase intruding Rock Ptarmigan, but we also observed the reverse in several cases. Ptarmigan males remain near females during pre-breeding and these chases may also have been related to mate guarding even in response to another species. These interactions combined with the potential to use similar habitats (see Table 3) suggest that interspecific competition likely contributes to a more restricted niche width for the two species. In Colorado, White-tailed Ptarmigan are the only species present

and appear to have a greater niche width, nesting from the treeline to the upper limits of vegetative cover (Braun et al. 1993; Wiebe and Martin 1998). Only Rock Ptarmigan are present in the European Alps, and Favaron et al. (2006) showed that territories were equally common in high altitude grassland, dwarfshrub vegetation and debris/early pioneer vegetation. This range of habitat appears to be greater than at our site, but caution is required as studies differ in habitat classification, and habitat structure varies among geographic locations. Weeden (1967, 1969) studied all three Ptarmigan species in Alaska and showed that different bill morphologies and winter diets likely reduce competition outside the breeding period. However, summer diets are much more varied and it is not clear that breeding habitat segregation would be influenced by food abundance, particularly for White-tailed and Rock Ptarmigan. Our observations suggest that these two species select similar foods in summer, although dependent on availability within territories (S. Wilson, unpublished data). Overall, it would appear that Ptarmigan habitat selection in this region is shaped by species-specific habitat preferences and interspecific territoriality, but further study would be useful. Removal experiments might allow for an examination of how one species expands its niche width in the absence of another, although this may be logistically difficult with continuous populations and constant replacement of individuals. An alternative would be to use density as a covariate and examine how niche width changes with natural fluctuations in the abundance of a competitor.

Intraspecific nest site selection

Within territories, females must select nest sites that offer protection from predators and weather. Weather extremes can be severe in open environments, which may affect hatching success or chick survival (Webb 1987), and can increase thermoregulatory costs of incubating females (Wiebe and Martin 1997). Individuals can compensate by selecting nest sites with a favorable orientation (With and Webb 1993; Nelson and Martin 1999), and this has been found to influence hatching success (Burton 2006). In our study, it was not possible to measure nest orientation because the scrapes Ptarmigan use do not face an obvious direction. However, using video cameras, we observed that females often switch directions during incubation (S. Wilson, unpublished data), which may allow them to compensate for changes in wind direction and the angle of solar radiation throughout the day. The tendency for females to nest on warmer west or south facing slopes would also offer thermoregulatory benefits.

Nest site cover is another means to increase protection from unfavorable weather, and we found that all three

species selected sites with higher lateral cover than expected at random. This finding is similar to that of other ground-nesting birds (Davis 2005), including grouse and Ptarmigan species (Schieck and Hannon 1993; Campbell et al. 2002; Holloran et al. 2005). Greater nest site cover may also reduce exposure to predators by lowering visibility of the female or reducing dispersion of her scent (Wiebe and Martin 1998). An earlier analysis revealed a slight positive influence of lateral cover on daily nest survival of Rock and White-tailed Ptarmigan at this site (Wilson 2008). We were unable to measure whether nest site cover offers thermoregulatory benefits to females, but this seems likely and could be tested further by examining whether lateral cover influenced the change in female condition over the incubation period. Some studies have also suggested that the benefits of nest cover may represent a tradeoff between nest and adult survival, with intermediate levels representing an optimal scenario that provides some nest protection while allowing females to avoid detection and being ambushed by predators (Götmark et al. 1995; Wiebe and Martin 1998).

While lateral cover was important, White-tailed and Rock Ptarmigan showed no tendency to select particular features (i.e., different ground cover types) for a nest site within territories. Although sample sizes were small, Willow Ptarmigan appeared more likely to nest in patches of low scrub birch rather than taller willows, likely because willow has a more open understory and nests would be more exposed to mammalian predators. At Chilkat Pass, British Columbia, approximately 200 km south of our study area, Willow Ptarmigan selected areas with higher lateral cover but showed no tendency for specific vegetation types (Schieck and Hannon 1993). Within the alpine zone, there may be less variation in how different ground cover types within a territory influence nest success, perhaps explaining why White-tailed and Rock Ptarmigan did not select particular features other than higher lateral cover. In such cases, random selection of a nest site may help prevent predators from developing a search image (Storaas and Wegge 1987; Schieck and Hannon 1993).

Zusammenfassung

Bruthabitatwahl sympatrisch vorkommender Weißschwanz-, Alpen- und Moorschneehühner im südlichen Yukon Territory, Kanada

Auf zwei Ebenen haben wir die Bruthabitatwahl von Weißschwanz- (*Lagopus leucura*), Alpen- (*L. muta*) und Moorschneehühnern (*L. lagopus*) an einem alpinen Standort in den Ruby Range Mountains im Yukon Territory, Kanada untersucht. Wir arbeiteten mit logistischer Regression, um

auf die artspezifischen Präferenzen schließen zu können, und verwendeten eine AIC-Modellselektion, um die einzelnen Nisthabitate von Weißschwanz- ($n = 43$) und Alpenschneehühnern ($n = 58$) zu vergleichen. Für das Moorschneehuhn ($n = 8$ Nester) beschränkten wir uns aufgrund kleinerer Stichproben auf deskriptive Statistik. Die Ergebnisse der Modellierung zeigen, dass die Höhe, das Gefälle und die Bodenbedeckung mit Gräsern und Flechten die Hauptvariablen bei der Trennung der Bruthabitate von Weißschwanz- und Alpenschneehuhn darstellen. Die mittleren Werte von Höhe und Gefälle um die Neststandorte der drei Arten folgte dem Muster Weißschwanzschneehuhn (1,827 m, 30°) > Alpenschneehuhn (1,728 m, 18°) > Moorschneehuhn (1,512 m, 6°). Das Weißschwanzschneehuhn wählte tendenziell trockenere, von Flechten, Felsen und Zwergsträuchern dominierte Habitate, wohingegen Alpenschneehühner häufiger auf Grasmatten mit eingestreuten baumartigen Sträuchern zu finden waren. Moorschneehühner nisteten in Bereichen dichter baumartiger Sträucher. Die drei Arten zeigen inter- und intraspezifische Territorialität. Während artspezifische Habitatpräferenzen eine Koexistenz der Arten zwar zulassen, wird die Nischenbreite jeder einzelnen Art durch die Anwesenheit der nahe verwandten Arten jedoch sicherlich schmaler, was in besonderem Maße für das Weißschwanz- und das Alpenschneehuhn gilt. Innerhalb der Reviere wählten alle drei Arten Neststandorte mit einer stärkeren Seitendeckung als stochastisch erwartet (24–50%). Weißschwanz- und Alpenschneehuhn wählten keine speziellen Deckungstypen (Vegetation oder Fels) für ihre Neststandorte im Revier, wohingegen sich die meisten Nester der Moorschneehühner in Beständen der Drüsigen Birke (*Betula glandulosa*) befanden.

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