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ARTICLE

Nonrandom territory occupancy by nesting Gyrfalcons (*Falco rusticolus*)

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Abstract: We know little regarding how specific aspects of habitat influence spatial variation in site occupancy by Arctic wildlife, yet this information is fundamental to effective conservation. To address this information gap, we assessed occupancy of 84 Gyrfalcon (*Falco rusticolus* Linnaeus, 1758) breeding territories observed annually between 2004 and 2013 in western Alaska. In line with the theory of population regulation by site dependence, we asked whether Gyrfalcons exhibited a nonrandom pattern of site selection and if heterogeneous landscape attributes correlated with observed occupancy patterns. We characterized high- and low-occupancy breeding territories as those occupied more or less often than expected by chance, and we evaluated land cover at 1 and 15 km circles centered around nesting territories to identify habitat variables associated with observed occupancy patterns. We tested 15 competing models to rank hypotheses reflecting prey and habitat variables important to nesting Gyrfalcons. We confirmed a nonrandom pattern of site selection but found only weak evidence that the distribution of prey habitat was responsible for this pattern. We reason that preferential habitat use by nesting Gyrfalcons may be determined by spatial scales other than those we measured or may be driven by landscape-level attributes at time periods other than during the brood rearing period.

Key words: Arctic raptor, *Falco rusticolus*, habitat quality, occupancy dynamics, population regulation.

Résumé : Nous en savons peu sur la façon dont des aspects particuliers de l'habitat influent sur la variation spatiale de l'occupation des sites par la faune arctique, mais cette information est essentielle à une conservation efficace. Pour combler cette lacune en matière d'information, nous avons évalué l'occupation de 84 territoires de reproduction du faucon gerfaut (*Falco rusticolus* Linnaeus, 1758) observés annuellement entre 2004 et 2013 dans l'ouest de l'Alaska. Conformément à la théorie de la régulation de la population par dépendance du site, nous nous sommes questionnés à savoir si les faucons gerfauts présentaient un modèle non aléatoire de sélection du site et si les attributs hétérogènes du paysage étaient corrélés avec les habitudes d'occupation observées. Nous avons caractérisé les territoires de reproduction à occupation élevée et faible comme étant ceux occupés plus ou moins souvent que prévu par hasard, et nous avons évalué la couverture terrestre à des cercles de 1 km et de 15 km centrés autour des territoires de nidification afin de déterminer les variables de l'habitat associées aux habitudes d'occupation observées. Nous avons évalué 15 modèles concurrents pour classer les hypothèses reflétant les variables relatives aux proies et à l'habitat importantes pour les faucons gerfauts nicheurs. Nous

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avons confirmé une habitude non aléatoire de sélection du site, mais n'avons trouvé que de faibles preuves que la répartition de l'habitat des proies était garant de cette habitude de sélection. Nous raisonnons que l'utilisation préférentielle de l'habitat par les faucons gerfauts nicheurs peut être déterminée par des échelles spatiales autres que celles que nous avons mesurées, ou peut être déterminée par des attributs au niveau du paysage à des périodes autres que la période d'élevage des couvées. [Traduit par la Rédaction]

Mots-clés : oiseau de proie d'Arctique, *Falco rusticolus*, qualité d'habitat, dynamique de l'occupation, régulation de la population.

Introduction

The regulation of animal populations is a central focus of ecology (Murdoch 1994). In a changing world, understanding population regulation is particularly relevant to wildlife management in which explaining species abundances, conducting conservation assessments, and designing adaptive management plans require baseline knowledge on population regulation. This is certainly true for the Arctic, where climate change is reconfiguring the biotic landscape, with as yet unforeseen consequences for wildlife populations (Tape et al. 2006, 2015). However, processes that regulate animal populations and influence patterns of occupancy are poorly understood for most Arctic species.

In heterogeneous landscapes, individuals often compete for sites that differ in suitability for reproduction or shelter (Fretwell and Lucas 1970; Wiens et al. 1987; Orians and Wittenberger 1991; Newton 1998; Byholm et al. 2007). Animals that preferentially settle in high-quality sites cause the best sites to be occupied more often than poor sites. As a population expands and good sites become fully occupied, some individuals must settle in poor sites where they experience low survival or decreased reproduction, thus lowering the growth rate of the population (Ferrer and Donazar 1996; Rodenhouse et al. 1997; Hunt and Law 2000). This preemptive use of sites in a heterogeneous landscape acts as a negative feedback mechanism on population sizes, thus regulating animal populations (Rodenhouse et al. 1997; Hunt and Law 2000). Empirical evidence for site-dependent population regulation often consists of observed patterns of occupancy that deviate from a random pattern and temporal or spatial variation in the distribution of environmental resources that affect habitat quality (Newton 1991; Sergio and Newton 2003). Indeed, Sergio and Newton (2003) reviewed 22 bird studies including 14 raptor species, all of which revealed nonrandom patterns of occupancy correlated with reproduction and other measures of territory quality, suggesting that site-dependent population regulation is common for predatory birds.

The Gyrfalcon (*Falco rusticolus* Linnaeus, 1758) is an apex avian predator of the Arctic tundra (Watson et al. 2011). Breeding as far north as 82°N latitude, it is considered a tundra specialist resident year-round at northern latitudes (Platt 1976; Nielsen and Cade 1990; Watson et al. 2011) and a dietary specialist dependent primarily on one or two bird species in the genus *Lagopus* (Roseneau 1972; Booms and Fuller 2003; Nielsen 2003; Nyström et al. 2006; Watson et al. 2011), although exceptions to these characterizations exist (Burnham and Newton 2011; Robinson et al. 2019). Because of its restricted range and diet, the Gyrfalcon is predicted to be one of the Arctic birds most vulnerable to climate change (Thomas et al. 2004; Liebezeit et al. 2012). Bente (2011) examined six consecutive years of occupancy data and observed variable spatial patterns of annual occupancy (e.g., variable site selection), suggesting high interannual mobility of breeding pairs characterized by low consecutive multiyear use of territories. This finding appears to contrast with occupancy patterns of other raptor species governed by site-dependent population regulation.

Therefore, clarifying site selection and habitat attributes of Gyrfalcons would inform science-based management.

The aim of this study was to test the two principle predictions of site-dependent regulation of Gyrfalcon populations. Based on 10 years of survey data from 855 distinct cliff sites in a 14 150 km^2 area on the Seward Peninsula, Alaska, we first asked whether occupancy patterns at breeding territories differed significantly from a random pattern. Certain territories being occupied significantly more often than others would suggest that some sites are preferred and thus suggest that the population is regulated by heterogeneity in territory quality. On the other hand, random patterns of occupancy would support arguments by Roseneau (1972) and Bente (2011) that unpredictable abiotic factors are principal in determining occupancy. We then modeled occupancy patterns from covariates describing attributes of prey habitat to see if heterogeneity in the biotic environment correlated with our observed occupancy patterns. Positive results from these analyses would confirm that Gyrfalcons breeding under unique pressures imposed by the harsh Arctic environment conform to site-dependent population regulation, similar to findings for other raptor species.

Methods

Study area and data collection

The Seward Peninsula in western Alaska is a rolling landscape of lowland and upland tundra interspersed with inland cliffs, numerous rock outcroppings, cliff-lined river systems, and mountainous terrain (Kessel 1979, 1989). The predominant vegetation class is low-lying tundra, with dense willow (*Salix* spp.), scrub birch (*Betula nana* L.), and alder (*Alnus* spp.) thickets along rivers and interspersed in valley bottoms and bare ground and rocky terrain on hilltops and at higher elevations. The climate is characterized by short summers and long winters.

We conducted comprehensive aerial surveys to inspect 855 previously catalogued cliffs and to determine occupancy by Gyrfalcon, Peregrine Falcon (*Falco peregrinus* Tunstall, 1771), Golden Eagle (*Aquila chrysaetos* (Linnaeus, 1758)), Rough-legged Hawk (*Buteo lagopus* (Pontoppidan, 1763)), and Common Raven (*Corvus corax* Linnaeus, 1758) within 14 150 km^2 of the Seward Peninsula (65.37°N, 164.22°W). All surveys used a Robertson R-44 helicopter as an observation platform between 13 June and 6 July during the years 2004–2011 and between 24–26 May and 20–26 June, respectively, during the years 2012 and 2013. Surveys were timed to determine raptor community occupancy among the five species with variable nest initiation dates and were therefore not optimal for any one species. Timing was also influenced by weather that either allowed or prevented flying. Based on phenology from age of nestlings estimated on surveys, Gyrfalcons in the study population initiate laying from 30 March to 19 May and eggs hatch from 5 May to 24 June. Therefore, occupancy surveys timed in June or early July missed an unknown number of nesting attempts that failed early. Although not ideal, this survey methodology was the best possible approach given local logistical and funding constraints. Aerial surveys consisted of frontal approaches to rock cliffs with the cliff face placed on the observer's side of the aircraft whenever possible and at close distance (50–200 m). Brief descriptive notes recorded by the observer for each cliff included cliff identity and location, species, number of birds, and nesting status.

Delineation of territories

The basic unit by which occupancy and productivity of raptors are measured is the nesting territory, and a nesting territory may include multiple alternative nesting sites (Sergio and Newton 2003; Millsap et al. 2015; Anderson et al. 2017). Because our data from

overflights were derived from individual sites, a first step in our analyses was to delineate territories and assign individual sites to territories. We used a set of decision rules based on observed occupancy rates and physiography to complete this process, as follows. Rule #1: If two nesting sites were separated by a distance of ≤1 km, they were considered alternative nesting sites in a single nesting territory. This rule was based on 473 distinct nesting observations for occupied Gyrfalcon nests in which the two minimum nearest neighbor distances that we observed during a single year were 0.8 and 1.0 km. Therefore, we felt that a distance of 1 km was a reasonable separation for distinct territories. Rule #2: If two sites within 1 km of each other were occupied in a given year, they were considered separate territories. Rule #3: In cases where multiple nesting sites were linked by distances of <1 km, physiographic breaks or discontinuities in cliff structure were evaluated with Rule #2 and were used to separate or group sites into territories. Figure 1 illustrates the decision process for four nesting sites linked by distances of ≤1 km and potentially considered a single nesting territory (Rule #1). Application of decision rules supported the delineation of two territories (Fig. 1).

Land cover data

Nesting site selection by birds occurs at different spatial scales (Wiens et al. 1987; Orians and Wittenberger 1991; Bruggeman et al. 2015). We therefore characterized prey habitat and escape cover around Gyrfalcon territories within 1 and 15 km circles centered on territories. In territories with multiple nesting sites, the circles were drawn around a point placed in the center and equidistant among nesting sites. We selected these distances a priori because 1 km is the minimum distance we used to separate Gyrfalcon territories, and 15 km represents an upper limit that male Gyrfalcons are thought to travel to provision nestlings (White and Cade 1971; Burnham and Burnham 2011).

We used data from the Alaska Gap Analysis Project (AKGAP) (60 m pixels) (Gotthardt et al. 2014) to determine the area of predicted habitat for two primary and five alternative prey species. We considered Willow Ptarmigan (*Lagopus lagopus* (Linnaeus, 1758)) and Rock Ptarmigan (*Lagopus mutus* (Montin,1781)) as primary prey species, based on the characterization of the Gyrfalcon as a dietary specialist on ptarmigan in western North America (Roseneau 1972; McCaffery et al. 2011; Mossop 2011). Habitat for Willow Ptarmigan and Rock Ptarmigan are clearly separable by physiography, plant species composition, and plant stature on the Seward Peninsula. Preferred habitat for Willow Ptarmigan consists of a patchwork of low shrubs 0.4–1.1 m in height dominated by *Salix pulchra* Cham., *Salix glauca* L., and *B. nana*, alternating with open spaces. This habitat occurs in valleys and other low-lying areas. Rock Ptarmigan habitat is characterized as barren fellfields at higher elevations and on windblown ridges, with a dwarf shrub mat <0.4 m tall of *Salix reticulata* L., *Empetrum nigrum* L., *Vaccinium* spp., *Saxifraga* spp., and *Dryas* spp. As alternative prey, we considered those species with a mass ≥100 g that were observed as prey in Gyrfalcon nests on the Seward Peninsula in 2014 and 2015 (Robinson et al. 2019) and for which AKGAP data were available (Arctic ground squirrel (*Urocitellus parryii* (Richardson, 1825)), Whimbrel (*Numenius phaeopus* (Linnaeus, 1758)), Long-tailed Jaeger (*Stercorarius longicaudus* Vieillot, 1819), American Golden-Plover, (*Pluvialis dominica* (Statius Muller, 1776)), and Pacific Golden-Plover (*Pluvialis fulva* (Gmelin, 1789)).

We used data from LANDFIRE (30 m pixels) (LANDFIRE 2013) to determine the extent of shrub habitat. We considered the extent of shrub cover as a proxy for escape cover and condensed data for five existing vegetation types (alder shrubland, avalanche shrubland, floodplain forest and shrubland, riparian stringer forest and shrubland, and willow shrubland) into a single covariate SHRUB (Table 1). We used ArcGIS version 10.2.0 (ESRI 2013) to

Fig. 1. Individual Gyrfalcon (*Falco rusticolus*) nest sites bound by distances of <1 km (ellipses) were assigned to breeding territories based on predetermined decision rules (see text). Three sites (504, 781, and 648) located on a single cliff were used in alternate years, supporting the view that they were alternative sites within a single nesting territory (Rule #1). Another site (285) was used concurrently with 504–781–648 (Rule #2). Nesting site sites 504, 781, and 648 were located on the same cliff face, whereas site 285 was located on a separate cliff band (Rule #3). Decision rules supported the delineation of two separate Gyrfalcon territories: 504–781–648 and 285. Map was generated using ESRI (2013). ArcGIS version 10.2.0 and based on data from U.S. Geological Survey (2015), Alaska, IfSAR Digital Elevation Model. Retrieved from http://ifsar.gina.alaska.edu/.
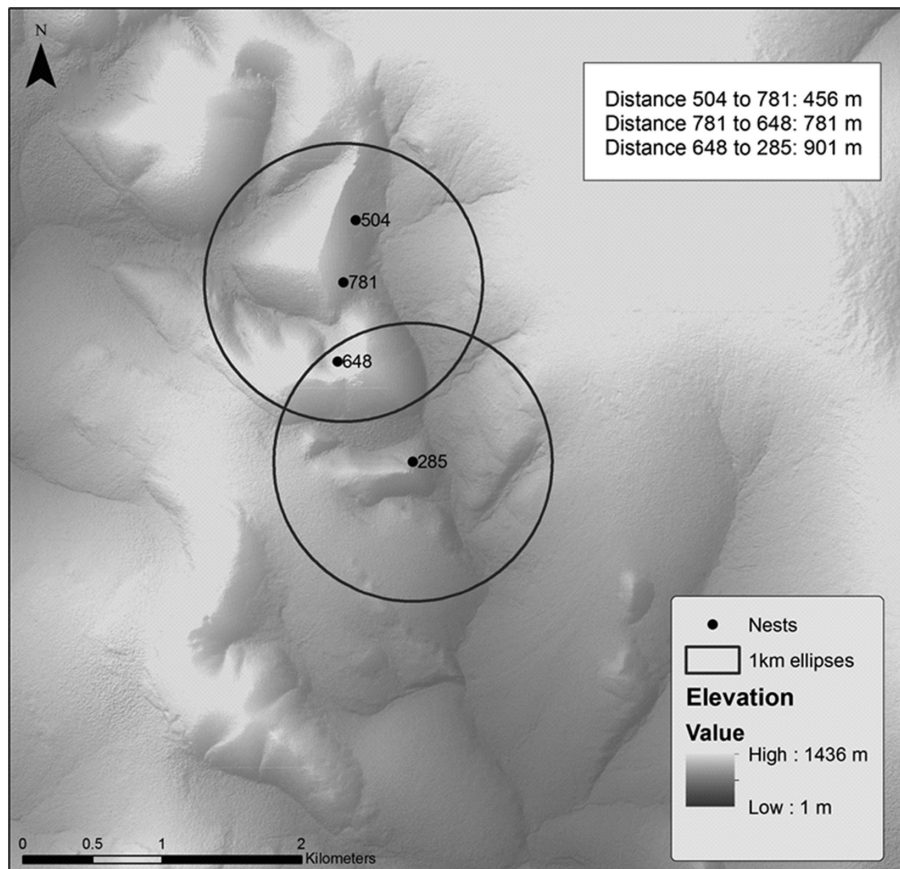
determine the area of prey habitat and shrub cover within the 1 and 15 km circles around nesting territories.

Our focus on macrohabitat (sensu Block and Brennan 1993) was a practical decision based on available data. Analyses involving Gyrfalcon productivity data would further illuminate occupancy patterns (Newton 1998), but consistently high-quality data were not available across all sites and years. Similarly, small sample sizes (e.g., 17 high-occupancy territories) limited the inclusion of intermediate spatial scales or additional variables such as variability in cliff-specific attributes.

Analyses

We identified high-occupancy territories within the study area through a multistep process as follows. When determining the expected number of years that a nesting territory was occupied, we set the probability of a site never being occupied at zero because, by

Table 1. Covariates hypothesized a priori to affect patterns of occupancy dynamics of Gyrfalcons (*Falco rusticolus*) nesting on the Seward Peninsula, Alaska, 2004–2013.

Covariate	Model	Rationale	Source(s) of hypotheses
Area of Willow Ptarmigan (*Lagopus lagopus*) habitat	WIPT	Willow Ptarmigan dominate the diet of Gyrfalcons in many parts of North America. Territories with a greater amount of Willow Ptarmigan habitat may provide greater prey availability near the nest, which would improve prenesting courtship and survival of young and lead to overall higher rates of occupancy	Roseneau 1972; Potapov 2011
Area of Rock Ptarmigan (*Lagopus mutus*) habitat	ROPT	Rock Ptarmigan are an important component of Gyrfalcon diet in parts of their range, including the Seward Peninsula. Populations of both species undergo cyclic fluctuations. Availability of Ptarmigan may augment Gyrfalcon diet during low points in the population cycle of Willow Ptarmigan. Greater amounts of Ptarmigan habitat may lead to higher occupancy rates	Roseneau 1972; Nielsen 2003, 2011; Mossop 2011
Area of Willow Ptarmigan and Rock Ptarmigan habitat	WIPT + ROPT	Gyrfalcons are described as dietary specialists of ptarmigan. The combined area of habitat for both ptarmigan species may lead to overall higher rates of occupancy than the area of either individual species	Nielsen 2011; Potapov 2011
Area of alternative prey habitat	ALT	Gyrfalcon breeding performance may correlate with an availability of nonptarmigan prey. Because the incidence of alternative prey in Gyrfalcon diet increases during low ptarmigan years, the availability of alternative prey may be important for sustained occupancy of Gyrfalcon territories. We included species >100 g and >10 detections in prey samples from the Seward Peninsula and for which habitat data were available	Burnham and Mattox 1984; Nielsen 1999; Booms and Fuller 2003; Robinson et al. 2019
Area of primary and alternative prey habitat	WIPT + ROPT + ALT	Gyrfalcon diet is broadest during the nesting season. Greater amounts of habitat for primary and alternative prey may provide a diverse diet needed to raise young successfully and influence territory selection	Potapov 2011
Area of shrubby escape cover	SHRUB	Prey vulnerability to predation may be more important than absolute abundance of prey in determining reproductive productivity in predators, including Gyrfalcons. Ptarmigan use shrub cover to escape from predators	Hannon et al. 1998; Nielsen 2003; Burgess et al. 2011; Mossop 2011
Global model	WIPT + ROPT + ALT + SHRUB	We tested the global model as a null hypothesis that none of the explanatory variables was more important in explaining patterns of Gyrfalcon occupancy	Burnham and Anderson 2002

Note: Listed are the covariates, models, the rationale for the respective hypotheses and citations forming the basis of various hypotheses. All models were evaluated at scales of 1 and 15 km buffers around 84 distinct breeding territories.

Table 2. Covariates, numbers of parameters (*K*), Akaike's Information Criterion (AIC) value, the difference in AIC between the model with the lowest AIC and a given model (ΔAICc), and Akaike weights (*w*ᵢ) for vector generalized linear models of Gyrfalcon (*Falco rusticolus*) territory occupancy at 84 territories on the Seward Peninsula from 2004 to 2013.

Scale (km)	Model	K	AICc	ΔAICc	w_i
1	ROPT	3	332.21	0	0.18
15	WIPT	3	332.38	0.17	0.16
NA	Null	2	333.01	0.8	0.12
15	ALT	3	333.51	1.3	0.09
15	WIPT + ROPT	4	334.28	2.07	0.06
1	WIPT + ROPT	4	334.4	2.19	0.06
1	WIPT	3	334.57	2.35	0.06
1	WIPT + ROPT + ALT	5	334.96	2.75	0.05
15	ROPT	3	334.99	2.78	0.04
15	SHRUB	3	335.04	2.83	0.04
1	ALT	3	335.09	2.88	0.04
1	SHRUB	3	335.15	2.94	0.04
15	WIPT + ROPT + ALT	5	336.07	3.86	0.03
1	WIPT + ROPT + ALT + SHRUB	6	337.27	5.06	0.01
15	WIPT + ROPT + ALT + SHRUB	6	338.04	5.83	0.01

definition, all territories had to be occupied at least once to be detected. We tested whether the pattern of observed occupancy differed from expected using a Fisher's exact test.

We tested hypotheses regarding potential landscape-level drivers of nesting territory occupancy by Gyrfalcons in two ways. First, we developed seven models from combinations of four covariates representing different hypotheses for nesting territory occupancy of Gyrfalcons (Table 1). We used vector generalized linear models (VGLM) with positive negative binomial distributions, which assign a probability of a site never being occupied as zero, using the VGAM package (Yee 2015) in R (R Core Team 2016). We built each model at the two spatial scales corresponding to the buffer sizes described above, and we also built a null, or intercept-only, model for a total of 15 models (Table 2). The models were built using the entire data set with the number of years occupied as the response variable. We ranked and compared models using Akaike's information criterion (Akaike 1974) corrected for small sample size (AICc) (Hurvich and Tsai 1989). We considered covariates as useful for inference if they were within models ΔAICc < 2 that did not contain uninformative parameters and were ranked above the null model (Burnham and Anderson 2002; Arnold 2010). Model selection based on AIC favors the retention of covariates with 85% confidence intervals that exclude zero (Burnham and Anderson 2002; Arnold 2010). Arnold (2010) therefore argued for the use of 85% confidence intervals when interpreting the results of models selected using AIC. To aid in interpretation, we thus present both sets of intervals and interpret cases where 85% or 95% confidence intervals exclude zero as marginal and strong evidence, respectively, of a correlation between occupancy and a given covariate (Ware et al. 2015; Bunkley et al. 2017).

Results

During the 10 year project period, we visited 855 distinct cliff sites and observed 473 Gyrfalcon nesting events at 232 distinct sites. On the basis of our decision rules, these nesting sites represented 84 breeding territories. Occupancy of individual territories ranged from 1 to 9 years, with 2 years being the median number of years a nesting territory was occupied.

The average occupancy of all territories surveyed in a given year was 0.30 (range = 0.13–0.43). The pattern of occupancy differed significantly from what would be expected under a positive Poisson pattern ($p < 0.01$; Fig. 2) (Sergio and Newton 2003). Territories at the extreme

Fig. 2. Observed and expected occupancy of Gyrfalcons (*Falco rusticolus*) at 84 breeding territories on the Seward Peninsula from 2004 to 2013. Expected frequencies were calculated from a positive Poisson distribution.
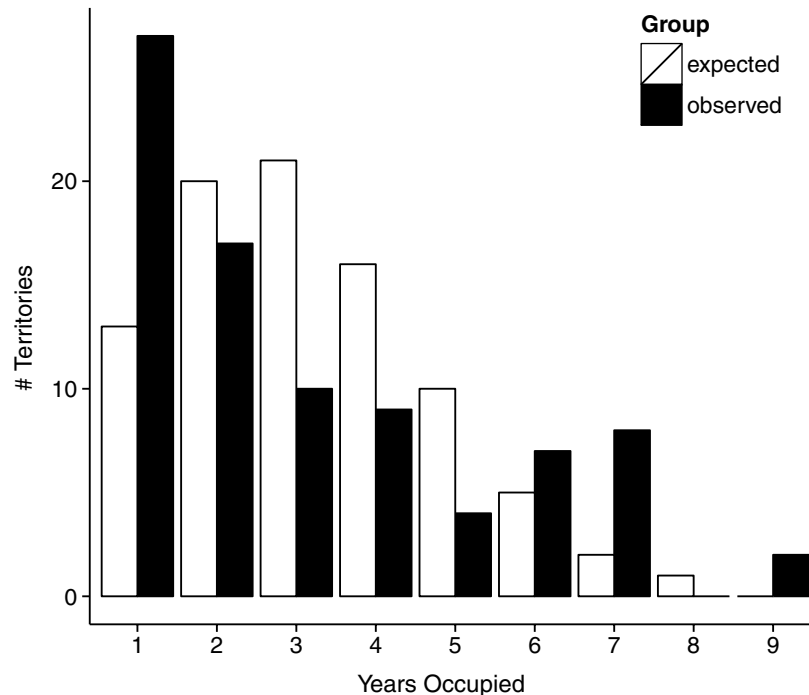
ends of the distribution — those occupied either 1 or ≥6 years — occurred more often than expected and we thus refer to them as the low ($n = 27$, 32% of all sites) and high-occupancy ($n = 17$, 20% of all sites) territories, respectively. Territories that were occupied 2–5 years ($n = 40$) occurred less often than expected (Fig. 2).

There was marginal evidence for associations between occupancy and measured covariates. The two models ranked highest by AICc represented habitat for ptarmigan species, although the null model was third-ranked and within ΔAICc < 2 (Table 2), indicating weak support for the two highest-ranked models. The AIC-best model indicated a negative relationship between the amount of Rock Ptarmigan habitat within 1 km ($\beta = -1.66$, 85% CI = −3.04 to −0.27) and territory occupancy, although the 95% confidence interval included zero (95% CI = −3.54 to 0.23) (Fig. 3). The second-best model indicated a positive effect of Willow Ptarmigan habitat within 15 km ($\beta = 1.81$, 85% CI = 0.24–3.37) (Fig. 4), also with 95% confidence intervals including zero (95% CI = −0.32 to 3.93). Variance inflation factors (VIF) for the most-parameterized models (Rock Ptarmigan + Willow Ptarmigan + Alternative + Scrub) (Table 1) indicated that any correlation between covariates did not hamper inference (VIF < 6) (Burnham and Anderson 2002). We further performed an a posteriori exploratory, all-subsets analysis (Doherty et al. 2012), but inference was the same as our a priori analysis. In further exploratory analysis, we tested our a priori models using covariates at the 5 km scale and found the null model was AIC-best.

Discussion

Our results confirmed a nonrandom pattern of site occupancy by nesting Gyrfalcons, in which 20% of sites were occupied more often than expected by chance and 32% of sites occupied less often than expected were avoided. Nonrandom site selection by Gyrfalcons

Fig. 3. The relationship (±SE) between multiyear Gyrfalcon (*Falco rusticolus*) territory occupancy and the proportion of Rock Ptarmigan (*Lagopus mutus*) habitat within a 1 km radius buffer, Seward Peninsula, Alaska, 2004–2013. Points represent raw data. The line and SE represent predictions from a VGLM model (Table 2).
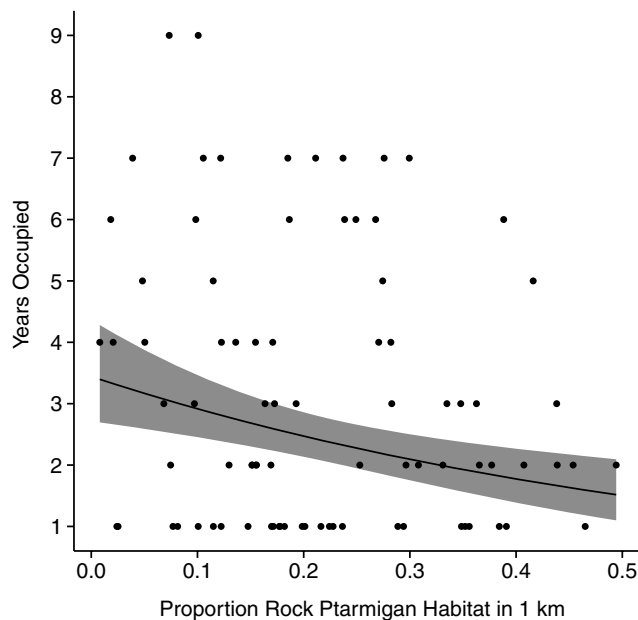
Fig. 4. The relationship (±SE) between multi-year Gyrfalcon (*Falco rusticolus*) territory occupancy and the proportion of Willow Ptarmigan (*Lagopus lagopus*) habitat within a 15 km radius buffer, Seward Peninsula, Alaska, 2004–2013. Points represent raw data. The line and SE represent predictions from a VGLM (Table 2).
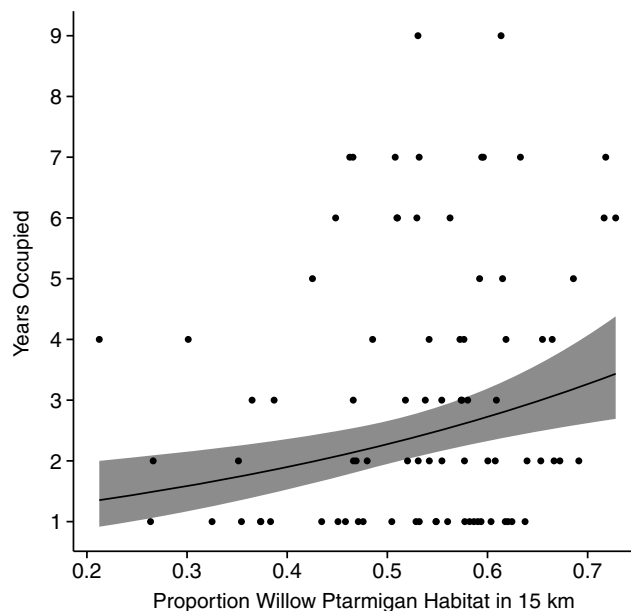
supports the first feature of site-dependent population regulation, namely preemptive use of preferred breeding sites. Our results also clarify findings by Bente (2011) from the same population in which the pattern of occupancy observed during consecutive years appeared not to support the premise of preemptive site selection.

Preemptive site selection is known for at least 14 species of raptors (Sergio and Newton 2003), where it conveys advantages for breeding and the successful fledging of young (Newton 1991). Although high-quality breeding sites often comprise a small proportion of all sites (Rodenhouse et al. 1997), by producing a surplus of nest-year recruits, they disproportionately contribute young to future generations (Hunt and Law 2000). Identifying such high-quality sites is useful in conservation planning because it improves our understanding of the biotic features needed to sustain populations, allows the prioritization of sites for protection or management, and helps to direct limited conservation dollars to the preservation of sites that sustain populations.

One principle advantage of high-quality sites is the availability of sufficient prey resources for successful reproduction. Landscape-level heterogeneity in habitat attributes such as prey resources, the second feature of site-dependent population regulation, then becomes a driver of preemptive site selection. Our results provided only weak support for the premise that landscape-level variables that we identified influenced territory occupancy by Gyrfalcons. In particular, the two top-ranked models of occupancy contained covariates of ptarmigan distributions that had 85% confidence intervals excluding zero. However, the null model was within ΔAICc < 2 and all 95% confidence intervals overlapped zero — indicating, at best, only marginal evidence for a correlation between Gyrfalcon occupancy and landscape-level covariates. We can therefore neither completely reject the hypothesis that Gyrfalcons select sites based on our measured covariates nor claim to have found robust patterns of habitat preference. The results of our habitat analysis are thus ambiguous and suggest that further study is warranted. We offer three potential explanations for our inability to identify habitat relationships.

First, site selection in Gyrfalcons may be occurring at a smaller scale than the landscape level that we examined. Preferential habitat use by wildlife occurs across multiple spatial scales, which for birds can be ranked by decreasing geographic area as landscape, territory, and nest (Luck 2002). Gyrfalcons forage widely across areas that overlap with neighboring pairs yet defend nest sites from conspecifics and competitors. This raises the question of whether site selection is less dependent on the distribution of prey resources and more a function of nest site attributes. Gyrfalcons begin nesting in late winter, and perhaps availability of nest sites with properties that protect the incubating female and nestlings from severe weather is a limiting factor. Alternatively, availability of nest sites may be dictated directly by weather events. Severe winter weather destroys stick nests and entire cliff ledges on the Seward Peninsula, and availability of suitable nest sites may be to some degree stochastic (Bente 2011).

Second, site selection may be occurring at the level of territory as we predicted, but we measured the wrong landscape-level variables, or else consider their importance at the wrong time of year. For instance, it is possible that prey availability during the courtships period, and not the brood rearing period as we hypothesized, may be driving the selection of nesting sites. Prey availability and energy demands of nesting Gyrfalcons vary during the course of the nesting season. During courtship in late March and early April, the level of energy reserves needed by the female to induce egg production is heavily influenced by prey availability and prey deliveries by the male at a period when the landscape is covered in snow and ptarmigan still occupy their winter ranges (Nielsen 2003). Prey availability during the brood rearing period is determined by the availability of ptarmigan on nesting territories and by the influx of migratory birds and seasonally available prey like squirrels,

which in turn will influence fledging success. Later in the year, densities of naive juvenile ptarmigan are thought to influence the survival of juvenile Gyrfalcons during dispersal (Nielsen 2003). Our focus on prey availability and habitat during the brood rearing period may have missed the period of critical prey limitation that influences nest site selection.

Finally, our attempt to describe prey habitat, and by extension prey availability, on the study area and in individual Gyrfalcon territories may have been flawed by a reliance on satellite data. Prior research has supported the validity of using Alaska GAP data for the purposes of this research (Cason et al. 2016) as well as the reliability of GAP species-habitat predictions at the landscape level (McClure et al. 2012; Steen et al. 2012). More research that correlates data from prey surveys (Hawkshaw et al. 2017) with occupancy patterns could shed further light on the subject. Because our findings support the premise of preferential habitat use by Gyrfalcons, we recommend further investigation into site selection at varying spatial scales and during times of the year outside the brood rearing period to improve our understanding of Gyrfalcon ecology.

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