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ORIGINAL ARTICLE

Landscape drivers of site occupancy by remnant populations of arctic ground squirrels (*Urocitellus parryii*)

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Abstract

Understanding habitat use by remnant populations of imperiled species can inform conservation efforts. Arctic ground squirrels (AGS; *Urocitellus parryii*) occupy alpine and boreal forest habitats in southwestern Yukon, Canada, where populations have been monitored since the 1970s. While alpine populations have remained stable, those in the boreal forest collapsed in the late 1990s and have not recovered. Propelled by the region-wide decline of AGS at low-elevation sites, our purpose was to document site occupancy by remnant populations and to identify habitats that are a high priority for monitoring and have potential for conservation. Using walking transects, we surveyed 155 sites in eight study areas for presence of AGS. Model-averaged occupancy probability was 0.643 (SE = 0.066), and the associated detection probability was 0.835 (SE = 0.075). AGS occurrence was strongly related to increasing habitat openness and also positively influenced by anthropogenic habitat and neighborhood occupancy. The availability of open habitat patches and connectivity among colonies within the boreal forest are consequential for the persistence of low-elevation populations of AGS. These factors may be linked to predator avoidance. Shrubification in the boreal forest as a result of climate warming may reduce AGS ability to detect and avoid predators. Recognizing anthropogenic habitats in land-use planning, and managing potential conflicts with landowners, may be important for the persistence and recovery of AGS at the southern edge of their range.

Keywords Boreal forest · Habitat model · Shrubification · Small mammals · Synurbic

Introduction

The distribution of species that exist as metapopulations reflects the interplay of habitat availability, local extinction, and colonization dynamics (Holt and Keitt 2000). The likelihood that a species occurs in a given area depends upon the quality and quantity of habitat at the local scale. However, habitat patches at broader spatial scales, including suitable but empty sites, can matter when a species is patchily distributed and local extirpations occur (Hanski and Gilpin 1997). Metapopulation dynamics may be particularly relevant for species with a heterogeneous distribution at the periphery of their geographical range, where their occurrence may be affected by reduced habitat suitability and decreased dispersal (Holt and Keitt 2000). Surveying the presence of species across habitat gradients allows us to recognize patterns and draw inferences about the relationships that may cause them (MacKenzie et al. 2006). Moreover, understanding habitat use by remnant populations of depleted species can inform measures for their conservation (Ball et al. 2005; Duggan et al. 2011; Logan 2016; Perkins-Taylor and Frey 2018).

The arctic ground squirrel (*Urocitellus parryii*; hereafter AGS) is a Beringian relict (Eddingsaas et al. 2004; Zazula et al. 2007; Galbreath et al. 2011) found in arctic and alpine tundra habitats across northwestern Canada, Alaska, and eastern Russia (Nadler and Hoffmann 1977), where they may be locally abundant. Less commonly, AGS occur in low-elevation boreal forest and meadow (grassland) habitats near the southern periphery of their range (Gillis et al. 2005; Donker and Krebs 2011; Wheeler and Hik 2013). Their occurrence in forested habitats is peculiar

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given that they evolved in open steppe habitats and survived the Last Glacial Maximum in ice-free refugia (Eddingsaas et al. 2004; Zazula et al. 2007; Galbreath et al. 2011). They are a colonial species that rely on being able to visually detect predators and vocally alert colony members of predation risks (Carl 1971; Hik et al. 2001; Wheeler and Hik 2014). Open habitats facilitate visual detection of predators, whereas forested habitats, or areas subject to significant shrubification, limit their ability to visually detect predators (Hik et al. 2001; Gillis et al. 2005; Wheeler and Hik 2014; Werner et al. 2016; Flower et al. 2019).

In the boreal forest of southwestern Yukon, Canada, AGS populations have been monitored since the 1970s (e.g., Boutin et al. 1995; Krebs et al. 2001). Between 1973 and 1999, low-elevation populations of AGS had cycled in concert with those of snowshoe hare (*Lepus americanus*; Karels and Boonstra 1999, Boutin et al. 1995). However, by 2000, the regional ground squirrel populations within the boreal forest had collapsed and have not yet recovered (Gillis et al. 2005; Werner et al. 2015a). Predation is the most likely proximate cause of the population collapse in low-elevation habitats (Werner et al. 2016). Several studies on low-elevation populations of AGS have shown that predation is a major limiting factor for AGS, especially when snowshoe hare densities are low and their predators, particularly lynx (*Lynx canadensis*), and coyotes (*Canis latrans*), turn to AGS as alternate prey (Karels and Boonstra 1999; Byrom et al. 2000; Karels et al. 2000). Coyotes may be of particular interest regarding the collapse of AGS in low-elevation habitats at the southern edge of their range, because they are a relatively new species to the ecosystem and a novel predator of AGS (Boonstra et al. 2018). Werner et al. (2016) used nearly 40 years of data from southwestern Yukon and found evidence for an unstable type II total predator response (Sinclair and Krebs 2002) that caused AGS populations to decline and remain at low levels, particularly in forested habitats, prompting uncoupling of AGS and snowshoe hare population cycles.

Despite being common in low-elevation habitats from the 1970s to 1999, more recently AGS densities in southwestern Yukon are highest in alpine tundra (5–6 squirrels/ha), low in low-elevation meadows (1.5 squirrels/ha), and lowest in forest (<0.5 squirrels/ha; Donker and Krebs 2011; Wheeler and Hik 2013; Werner et al. 2015a). AGS might display source-sink population dynamics among these habitats, where forest habitat functions as a population sink, and adjacent low-elevation meadows as population sources (Gillis et al. 2005). However, at present, there is no evidence that AGS from alpine tundra populations disperse downhill to colonize lower elevation habitats (Donker and Krebs 2012; Gillis et al. 2005). Surveys of AGS occurrence in 2008–2013 indicated that most colonies (>90%) in alpine tundra and anthropogenic habitats (e.g., agricultural and other land clearings, roadside verges) were occupied, but fewer colonies in low-elevation meadows (45%) and forest (4%) were occupied (Werner et al. 2015a; Werner 2016). Persistence of AGS colonies near human activity does not fit the general pattern of declining population density and colony occupancy at lower elevations (Werner et al. 2015a). The reasons for this anomalous pattern in anthropogenic habitats are not well understood.

Propelled by the region-wide collapse of AGS at low-elevation sites in southwestern Yukon (Gillis et al. 2005; Donker and Krebs 2011; Werner et al. 2015a), our purpose was to document site occupancy of remnant populations of AGS in areas with low-elevation meadows so that we can identify areas to focus conservation and monitoring efforts. First, we assessed the suitability of our survey design for monitoring occupancy of AGS, with an eye toward potential applicability to other burrowing, and apparently conspicuous, sciurids. Occupancy surveys have been informative for providing data useful for conservation of similar species (e.g., Ball et al. 2005; Duggan et al. 2011; Logan 2016; Perkins-Taylor and Frey 2018; Kukka et al. 2020). Second, we determined baseline estimates of AGS occupancy in landscapes containing open areas that were likely suitable habitat and harbored remnant populations in southwestern Yukon, after the population collapse in the late 1990s. Third, and most pointedly, we used an occupancy modeling approach to examine how factors related to habitat suitability and dispersal influence AGS distribution in low-elevation habitats. Because increased predation (Werner et al. 2015a, 2016) and predator-induced stress (Hik et al. 2001; Werner et al. 2015b) have been implicated as likely causes of the population decline, we developed a priori candidate models to explain site occupancy that incorporated landscape characteristics based on the apparent security they provided to AGS. Specifically, we predicted that AGS occupancy would be positively related to the percent of open habitat and anthropogenic habitat and negatively related to linear features and edge habitat, because these covariates likely influence predation risk. Because AGS may exhibit metapopulation structure (Donker and Krebs 2012), we also tested the hypothesis that site occupancy was a function of landscape context. We predicted that the occurrence of AGS at nearby sites would increase site occupancy because periodic extinctions of colonies could be followed by recolonizations. From these hypotheses, we built candidate models to estimate the importance of different factors on the probability of AGS occupancy at low-elevation habitats at the southern edge of their range.

Methods

We conducted this study in the Boreal Cordillera Ecozone in southwestern Yukon, Canada. Our study area was a wilderness landscape, comprised largely of boreal forest, but was increasingly becoming settled and developed (Thomas et al. 2021). The area was characterized by complex topography including mountain ranges, alpine plateaus, and lowland valleys that are largely forested. The climate was subarctic, semi-arid, and strongly seasonal. The annual precipitation ranged from 250 to 600 mm, which mostly fell as snow from October to May. The mean monthly temperature for July—the height of the active season for AGS—ranged from 10 to 15 °C (Smith et al. 2004). Because we were specifically interested in the occupancy of depleted, low-elevation populations of AGS, we limited our study to large lowland valleys, with elevations ranging from 600–900 m, where the habitat is predominantly open canopied boreal forest dominated by white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*). Open xeric meadows are common on south-facing slopes and post-fire (> 50 years ago) valley bottoms that have yet to regenerate (Burn 1998; Hogg and Wein 2005). Anthropogenic habitat in our study area was largely limited to an approximately 1-km-wide corridor along the Alaska Highway (Fig. 1), where small patches of agricultural and residential developments, as well as a few major linear features, such as utility lines and roadside verges, were interspersed within a matrix of natural habitat (Thomas et al. 2021). In addition to AGS, other common small mammalian herbivores included red squirrel (*Tamiasciurus hudsonicus*), least chipmunk (*Tamias minimus*), snowshoe hare, and several species of arvicoline rodents. Potential mammalian and avian predators of AGS included lynx, red fox (*Vulpes vulpes*), coyote, wolf (*Canis lupus*), grizzly bear (*Ursus arctos*), wolverine (*Gulo gulo*), northern goshawk (*Accipiter gentilis*), red-tailed hawk (*Buteo jamaicensis*), bald eagle (*Haliaeetus leucocephalus*), and golden eagle (*Aquila chrysaetos*).

AGS at low elevations in our study area are typically associated with meadows, fields, and open slopes, although from the 1970s to 2000, they were also common in forested habitats (Werner et al. 2015a, 2016). Using satellite imagery, we identified eight survey blocks, each 9 km^2, along a 235-km route along the Alaska Highway in southwestern Yukon (Fig. 1) that included open habitat types at low elevations. Survey blocks were a mean of 31 ± 24 km (SD) apart. Using ArcGIS 10.3 (ESRI, Redlands, CA, USA.), we randomly distributed 20 survey points within each of the survey blocks ($n = 160$ points; Fig. 1). For each survey point, we designed a triangular transect for sampling AGS, with each side 125 m long, and the triangle encompassing an area of 0.7 ha (hereafter “site”; Fig. 1; Supplemental Information Table S1). Because we were interested in quantifying AGS site occupancy at the colony level, we spaced sites ≥ 500 m apart to increase likelihood of meeting the assumption of independence between sites. This distance exceeds routine movement and mean dispersal distance of AGS (Byrom and Krebs 1999; Donker and Krebs 2011).

Typically, AGS are conspicuous and amenable to walking transects aimed at detecting presence. Specifically, their burrows often have mounds of displaced soil that are easily observed, and individual AGS typically stand vigilant at their burrow entrances and vocalize at the presence of humans. We sampled each site twice between 15 June and 18 September 2015, using walking transects. The mean time between sampling periods at each site was 18 ± 12 days. Each site was surveyed by a single observer who walked the perimeter of the triangle, using a handheld Global Positioning Satellite (GPS) receiver to navigate to the vertices of the triangle. Observers actively looked and listened for AGS or their burrows while traversing the triangular transects. A site was scored as occupied if AGS were unambiguously

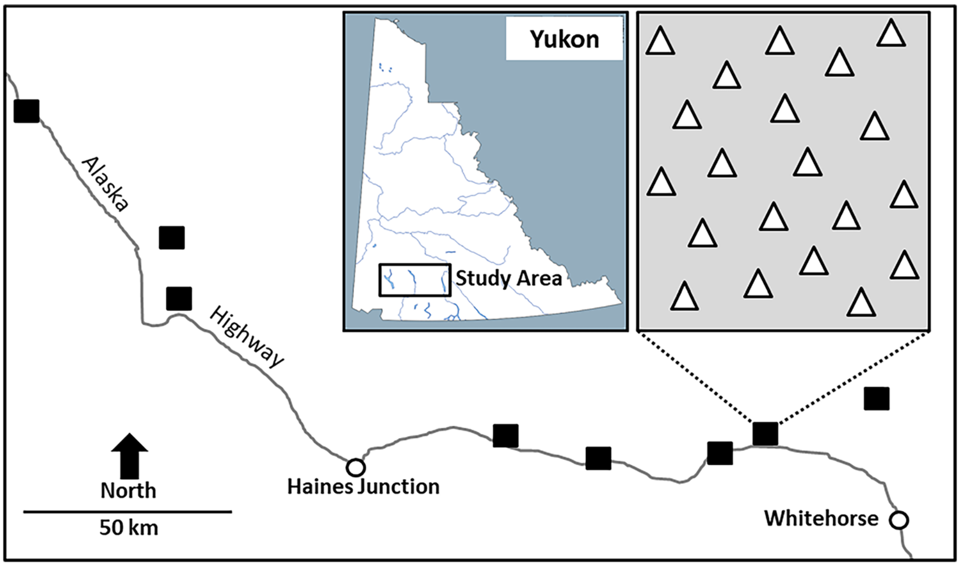

Fig. 1 Location of survey blocks (black squares, $n = 8$), and placement of random survey sites ($n = 20$; right inset map) within each block to determine Arctic ground squirrel (*Urocitellus parryii*) site occupancy. Each triangle in the inset map represents a sampling site within each 3 km × 3 km survey block. Dark grey line is the Alaska Highway, and white dots are major communities in the study area. The left inset map shows the location of the study area within southwestern Yukon, Canada

Table 1 Predictor variables (covariates) expected to influence site occupancy for Arctic ground squirrel (*Urocitellus parryii*) in southwestern Yukon, Canada, their relationship to fitness for the species, the observed range of values, and our a priori prediction of their direction of impact

Covariate	Relationship to fitness	Range of values (mean)	Predicted relationship
Open habitat on site (%)	Visual detection of predators, plant phenology	0–95 (28.3)	Positive
Anthropogenic habitat on site (%)	Predator avoidance, introduced forage, disturbed soils for burrowing	0–45 (3.5)	Positive
Linear features (absent = 0/present = 1 on site)	Predator movement	0–1 (0.3)	Negative
Edge habitat (count of sharp edges between open and canopied habitats along transects: 1 = full canopy to low edge, 2 = moderate edge 5–10; 3 = high edge > 10)	Predator concealment, vigilance	1–3 (1.9)	Negative
Neighborhood (Mean model-averaged occupancy of AGS at the3 nearest sites)	Recolonization	0.40–0.84 (0.64)	Positive

seen or heard, or if active burrows were present, during any part of the survey of the site. Active burrows were defined as having fresh diggings, paw prints, or scat. To meet model assumptions of independence between surveys, each survey was discrete and observers did not use prior knowledge of AGS detection or non-detection to influence searches or to determine presence. The relatively short time between our surveys at each site further ensured that our design likely met the assumptions of independence between surveys by reducing the likelihood an individual AGS that would disperse from a site during the interval between surveys.

We measured covariates at each survey site that may influence survival and fitness of AGS and formed a priori predictions of their influence on probability of AGS occupancy (Table 1). Covariates included the percent of open habitat and anthropogenic habitat, presence of anthropogenic linear features, an index of edge habitat, and the surrounding (neighborhood) occupancy of AGS (Table 1). Because we were interested in how covariates influence site occupancy at the colony level, we estimated the predictor variables within a 100-m radius (3.14 ha) of the centroid of each triangle, using recent high resolution (< 0.5 m) satellite imagery and aerial photographs. Estimations of land-cover type for each site were validated by inspection during field surveys. We estimated the percent of open habitat at each site, which is considered more suitable for AGS than closed canopy habitat (Karels and Boonstra 1999; Hik et al. 2001; Flower et al. 2019). We quantified the percent of anthropogenic habitat (e.g., infrastructure, industrial clearings and excavations, and cultivated fields), because anthropogenic disturbance can provide improved visibility, forage, and burrowing material, as well as deter predators (Berger 2007; Werner et al. 2015a). We also recorded the presence of anthropogenic linear features (e.g., highways, dirt roads, and power lines), because linear features may increase predation risk for AGS by facilitating predator movements between AGS colonies. Additionally, we estimated the amount of edge between open and closed canopy habitat, because edge habitats may conceal approaching predators (Hackett 1987) and harbour predators that focus on edge habitats (Theberge and Wedeles 1988; O'Donoghue et al. 1997; Salek et al. 2010). Increased hunting success by predators along forest edges was found to cause greater territorial vacancies in colonies of Columbian ground squirrel (*Urocitellus columbianus*; Hackett 1987). We visually counted hard edges between open and closed canopy habitat types along 5 parallel transects oriented north to south and spaced 33 m apart within the 100-m buffer around each survey site.

Table 2 Model selection results for factors influencing the detection probability (p) of Arctic ground squirrels (*Urocitellus parryii*) in southwestern Yukon, Canada. Survey covariates include date (D), temperature (T), observer (Ob), and open habitat (O). Arctic ground squirrel occupancy (Ψ) is held constant. Models with $\Delta\omega > 0.95$ are reported, and the null model (.) is included for comparison. Number of sites = 155

Model	ΔAICc	ω	k	-2L
$\Psi(.)\ p(O, D, T)$	0.00	0.408	5	316.64
$\Psi(.)\ p(O, D, T, Ob)$	2.13	0.141	6	316.60
$\Psi(.)\ p(O, T)$	2.49	0.118	4	321.26
$\Psi(.)\ p(O, D)$	3.57	0.069	4	322.34
$\Psi(.)\ p(D, T)$	3.76	0.062	4	332.53
$\Psi(.)\ p(O)$	4.12	0.052	3	325.00
$\Psi(.)\ p(O, T, Ob)$	4.49	0.043	5	321.13
$\Psi(.)\ p(O, D, Ob)$	5.66	0.024	5	322.30
$\Psi(.)\ p(D)$	5.76	0.023	3	326.64
$\Psi(.)\ p(D, T, Ob)$	5.88	0.022	5	322.52
$\Psi(.)\ p(.)$	8.98	0.005	2	331.94

Difference in AICc values between each model (ΔAICc); model weight (ω); number of parameters in the model (k); and twice the negative log-likelihood (2L)

Table 3 Model selection results for factors influencing site occupancy (Ψ) for Arctic ground squirrel (*Urocitellus parryii*) in southwestern Yukon, Canada. Covariates included open habitat (O), anthropogenic habitat (A), linear features (L), edge habitat (E), and neighborhood occupancy (N). Models with $\Delta\omega > 0.95$ are reported, and the null model (.) is included for comparison. A general model ($\Delta\omega > 0.95$) for detection probability, *p* (date, temperature, observer, open habitat), was included in all Ψ models. Model-averaged estimates of Ψ, *p*, and associated standard errors (SE) are provided. Number of sites = 155

Model	ΔAICc	*ω*	k	Ψ	SE	*p*	SE	-2L
Ψ(O,A)	0.00	0.250	8	0.643	0.063	0.837	0.075	299.23
Ψ(O)	1.06	0.147	7	0.643	0.055	0.835	0.075	302.52
Ψ(O,A,N)	1.84	0.100	9	0.643	0.072	0.835	0.075	298.82
Ψ(O,A,E)	2.08	0.088	9	0.644	0.074	0.835	0.076	299.06
Ψ(O,A,L)	2.24	0.082	9	0.642	0.073	0.837	0.075	299.22
Ψ(O,L)	2.58	0.069	8	0.642	0.066	0.837	0.075	301.81
Ψ(O,N)	2.60	0.068	8	0.645	0.065	0.835	0.075	301.83
Ψ(O,E)	3.26	0.049	8	0.643	0.066	0.835	0.075	302.49
Ψ(O,L,N)	3.70	0.039	9	0.643	0.075	0.835	0.075	300.68
Ψ(O,A,N,L)	4.02	0.034	10	0.643	0.081	0.836	0.075	298.71
Ψ(O,E,N)	4.77	0.023	9	0.645	0.075	0.832	0.076	301.75
Ψ(.)	12.95	0.000	6	0.683	0.051	0.783	0.082	316.60
Model average				0.643	0.066	0.835	0.075	

Difference in AICc values between each model (ΔAICc), model weight (*ω*), number of parameters in the model (k), and twice the negative log-likelihood (-2L)

Finally, we estimated the neighborhood occupancy of AGS at each site as the mean of the weighted model-averaged estimate of occupancy of the three closest sites. Occupancy estimates for this step were from models assessing the four local habitat covariates and using methods described below (Supplemental Information Table S2). Proximity of active colonies determines the probability of recolonization after local extinction (Hanski 1998, 1999) and persistence of AGS in sink habitats (Gillis et al. 2005).

We considered four covariates that may influence the detectability of AGS: date of survey, ambient temperature, habitat openness, and observer. To account for differences in AGS detectability that may arise from seasonal changes, we used sequential increasing numbers to represent survey dates between 9 June (“1”), and 27 September (“111”). Considering that temperature may influence AGS activity above ground, and therefore detectability, we recorded the ambient temperature for each survey. Given that habitat openness may influence the detectability of AGS, we included our covariate for open habitat (described above). Finally, we considered that observer experience may influence AGS detectability by recording a “1” for surveys completed by an experienced observer and a “0” for surveys conducted by less experienced observers.

We developed single-season occupancy models in program Presence (version 10.9; Hines 2006) to estimate the probability of AGS detection (*p*) and site occupancy (Ψ). Akaike’s information criterion, adjusted for small sample sizes (AICc; Burnham and Anderson 2002), was used in the model selection procedure to rank the relative support for different models in order of parsimony, with effective sample size defined as the number of sites. Parameter estimates were obtained from a 95% model set (summed model weight [$\Sigma\omega$] > 0.95). We considered models with ΔAICc < 2 to have strong empirical support, and covariates with high summed model weights were considered most influential at determining AGS occurrence and detectability. Beta-coefficients were used to determine the strength and direction of impact of covariates on detectability and occupancy of AGS (Burnham and Anderson 2002).

We first considered covariates for detection probability. We considered all possible combinations of survey covariates ($n = 15$ models), while holding occupancy constant. Survey covariates from the top models (ΔAICc < 2) were included in all subsequent analyses of AGS site occupancy.

To determine the factors that best explain AGS occupancy, we compared all possible combinations of site

Table 4 ß-coefficients and standard errors (SE) for covariates potentially influencing site occupancy of Arctic ground squirrel (*Urocitellus parryii*) in southwestern Yukon, Canada. Covariates are ranked according to their relative contribution (summed model weights $\Sigma\omega$). Covariates with robust impact (ß ± 1.96 × SE not overlapping zero) are indicated with bold

Covariate	ß-coefficient	SE	Σ*ω*
Open habitat	**0.844**	**0.250**	0.95
Anthropogenic habitat	0.551	0.425	0.58
Neighborhood occupancy	0.197	0.187	0.35
Linear features	−0.217	0.204	0.24
Edge habitat	0.088	0.297	0.21

covariates ($n = 31$ models). We calculated the Pearson's correlation coefficient for all covariates prior to inclusion into models and excluded any covariates with $r < \pm 0.5$, which we considered a reasonable cut-off for moderate to strong correlation (Mukaka 2012). All covariates were normalized prior to analyses through z-transformation. We assessed the goodness-of-fit of the general model with Chi-square tests and 10,000 bootstrap samples (MacKenzie et al. 2006).

To inform design of future occupancy surveys for AGS, we calculated the minimum number of surveys required to infer absence with a given certainty. The probability of detecting AGS at least once at an occupied site after k repeat surveys is calculated as Pk = 1 – (1 – p) k where P is the per-survey detection probability (MacKenzie and Royle 2005). Following this, the minimum number of surveys required (Nmin) to infer AGS absence with a 99% certainty (Kéry 2002) is calculated as Nmin = log(0.01)/log(1 – p).

Results

We surveyed 155 sites (five sites were excluded due to flooding; Supplemental Information Table S1). AGS were detected ≥ 1 time at 96 sites, resulting in a naïve occupancy rate of 0.619. Given presence at a site, the probability of detecting AGS on a single survey was high ($p = 0.835$; SE = 0.075) but < 1, resulting in a weighted model-averaged occupancy probability (Ψ) of 0.643 (SE = 0.066). Our estimate is 4% higher than the naïve estimate, which does not account for detection error.

Detection probability (p) of AGS was best explained by the amount of open habitat (Σω = 0.86), temperature (Σω = 0.79), and survey date (Σω = 0.75; Table 2). The probability that AGS would be detected on a survey was positively related to habitat openness (ß = 0.875, SE = 0.385), and negatively related to temperature (ß = –0.683, SE = 0.282) and progression in season (ß = –0.547, SE = 0.276). We found no evidence of observer bias on detection probability (ß = 0.085, SE = 0.423).

AGS occupancy (Ψ) was strongly determined by open habitats (Σω = 0.95). Anthropogenic habitat and neighborhood occupancy also affected AGS occupancy (Σω = 0.58 and 0.35, respectively), whereas linear features and edge did not (Tables 3 and 4). The probability that AGS occupied a site strongly increased with increasing habitat openness (ß = 0.844, SE = 0.250). Based on the model-averaged ($\Sigma\omega = 0.95$) site-specific estimates, mean AGS occupancy ranged from 0.40 (± 0.08 SE) at sites without open habitat to 0.94 (± 0.05) at sites where open habitats exceeded 75% (Fig. 2). AGS occupancy was also generally higher at sites with more anthropogenic habitats (β = 0.551, SE = 0.425) and at sites with a greater surrounding neighborhood occupancy (ß = 0.197, SE = 0.187; Table 4). There was no evidence of lack of fit ($P = 0.33$) or over-dispersion ($\hat{c} = 1.15$) in our global model (Burnham and Anderson 2002; MacKenzie et al. 2006). Correlation among covariates was low

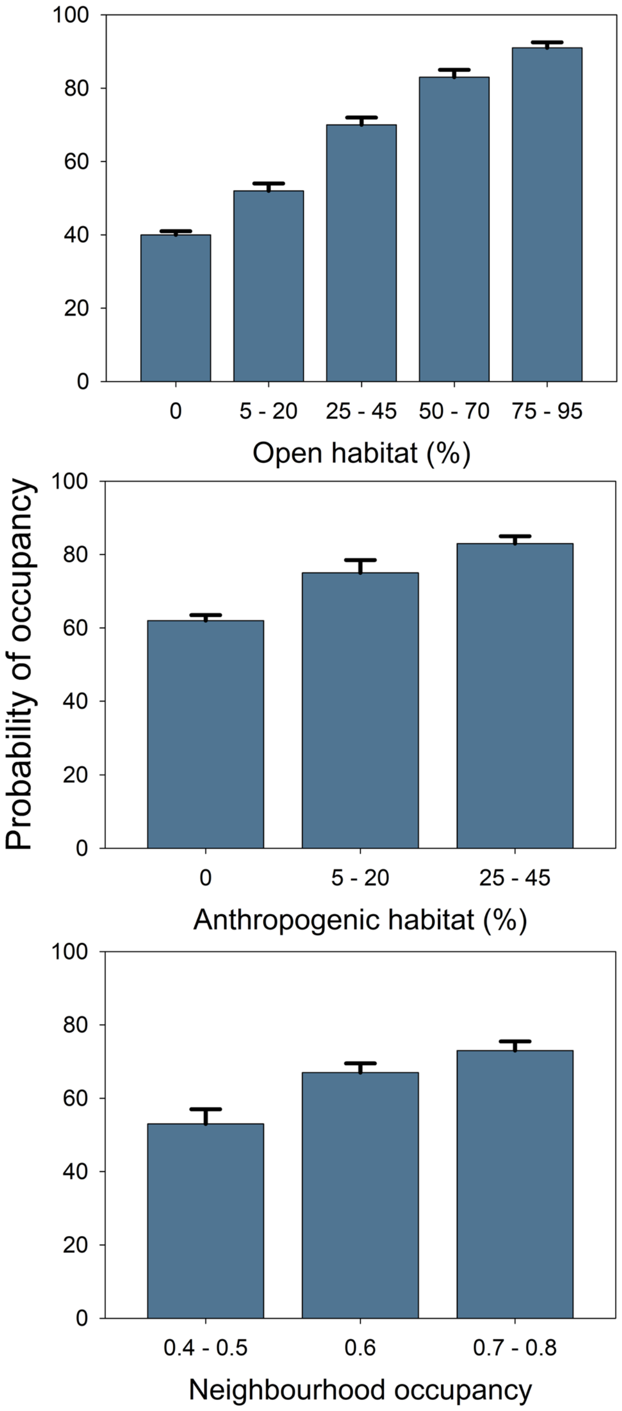

Fig. 2 Influence of open habitat, anthropogenic habitat, and neighborhood occupancy on probability of site occupancy ($n = 155$) for the Arctic ground squirrel (*Urocitellus parryii*) in southwestern Yukon, Canada. Estimates of site occupancy are based on the averaged model ($\Sigma\omega > 0.95$). Bars represent standard error

with the greatest being between our anthropogenic and linear covariates ($r = -0.44$).

Based on the model-averaged estimate of AGS detection (0.835) and the number of surveys we conducted per site ($n = 2$), the power of our study was $1\text{-}(1-0.835)^2 = 0.97$. We could confirm AGS absence with 97% certainty. Our results indicate that three repeat surveys of sites are required to confirm AGS absence with 99% certainty ($\text{Nmin} = \log(0.01) / \log(1 - 0.835) = 2.56$).

Discussion

Given recent region-wide declines in low-elevation populations of AGS at the southern edge of their range (Werner et al. 2015a, 2016), our study provides a framework for documenting site occupancy, and a baseline to monitor future change, at a regional level. One caveat is that our measure of naïve site occupancy was high (62%) because we located our study blocks in areas where we anticipated that remnant populations occurred. The naïve occupancy from randomly chosen blocks would have been lower (Donker and Krebs 2011; Werner et al. 2015a). However, we recommend that the priority for regional monitoring programs of AGS should focus on documenting changes to remnant populations at periodic intervals to assess population trends.

We found that walking short, triangular transects, coupled with occupancy modeling, was an efficient and cost-effective means to non-invasively monitor AGS at both site and regional levels. While AGS are generally detectable due to both their alarm calls and conspicuous burrows, habitat openness affected their detectability. In addition, high diurnal temperatures and the progression of summer decreased their detectability likely due to decreased activity above ground. This result is intuitive because AGS adjust their behavior to avoid thermal stress and to decrease both their metabolism and above ground activity as summer progresses (Long et al. 2005; Williams et al. 2012, 2016; Sheriff et al. 2013). We found that observer experience did not influence detectability of AGS, in contrast to studies on other species that are also considered readily detectable, such as American pika (*Ochotona princeps*; Moyer-Horner et al. 2012). Periodic monitoring of AGS distribution via occupancy assessment should use standardized protocols that limit surveys to time periods when above ground activity of AGS is maximal and weather conditions are optimal (< 25°) to reduce detection variance during field studies.

Several species of small mammals are of conservation interest because they are locally imperiled (Ball et al. 2005; Magle and Crooks 2009; Duggan et al. 2011; Logan 2016; Perkins-Taylor and Frey 2018; Kukka et al. 2020). Conversely, some local populations may be of management interest because of human-wildlife conflicts (e.g., Van Vuren et al. 1997). Aspects of our protocol may be suitable to monitor other vocal species of small mammals as well, but we recommend testing applicability prior to embarking on long-term monitoring initiatives.

Our results indicated that AGS occupancy was strongly determined by coverage of open habitats. AGS occupied both open meadow and forest habitats, but they were up to three times more likely to occupy sites that were mostly open compared to sites that were mostly covered by trees or shrubs. Although we did not measure vertical vegetation cover, openness of understory is also likely a relevant factor for forest-dwelling AGS (Wheeler and Hik 2014). Karels and Boonstra (1999) found that within forests, occupancy of burrows by AGS may be partially predicted by visibility. However, habitat selection by AGS is likely more complicated than a simple choice of open habitat patches. The historic distribution of AGS in meadows, forest, and human-modified landscapes indicates that AGS are flexible in their use of habitat. Notwithstanding this adaptability, habitat-specific patterns in body condition (Werner et al. 2015b), stress levels (Sheriff et al. 2012), survival and reproduction (Donker and Krebs 2012), and population distribution and abundance (Donker and Krebs 2011; Werner et al. 2015a; this study) indicate the importance of habitat quality.

Anthropogenic habitat had a moderate, positive effect on AGS occupancy. Modified habitats may provide high quality habitat for AGS as a result of vegetation clearing and maintenance at a cropped height, improved forage and soils for burrowing, and through better detection and avoidance of predators. Predators may also avoid anthropogenic habitats, particularly in areas of frequent human activity. Conversely, predators (including pets) may also be more abundant in anthropogenic habitats, resulting in higher predation rates. Our results support the finding by Werner et al. (2015a) that AGS populations near human activity have not declined at the same rate as other low-elevation populations in southwestern Yukon. AGS populations may benefit from proximity to humans and thrive in modified landscapes. However, populations that rely on human-modified habitat may quickly decline if land use practices change or increase in intensity, AGS are perceived as "pests" by landowners, or predation rates increase. Thus, while some anthropogenic habitats may be attractive to AGS, they may become an ecological trap and harbor sink populations (e.g., Remes 2000; Delibes et al 2001; Schlaepfer et al. 2002; Hoffman et al. 2003).

AGS occupancy was also explained by the increasing presence of conspecifics in the surrounding landscape, indicating that connectivity among colonies may be a factor for AGS distribution. Connectivity among local populations is generally influenced by the distance between existing populations and the nature of the habitat between them (Hanski

1998, 1999). Conspecific attraction may be important for successful recolonization. For example, Weddell (1991) found that dispersing Columbian ground squirrels settled in or near other squirrels rather than vacant habitats. Similarly, colony connectivity was the strongest predictor of site occupancy for black-tailed prairie dogs (*Cynomys ludovicianus*) along a gradient of urbanization (Magle and Crooks 2009). Because dispersers in AGS populations are typically males (Byrom and Krebs 1999; Naughton 2012), they may be particularly attracted to already occupied habitats for mating opportunities. Recolonization opportunities after population collapses may also fail due to an Allee effect (Allee 1931) caused by the disruption of social signaling of approaching predators when few individuals occupy a colony (Werner et al. 2016).

Habitat models alone may not accurately predict AGS occurrence without incorporating additional intra- and interspecific interactions (e.g., conspecific attraction and predator–prey relationships). For instance, social factors can influence habitat selection by wildlife (Campomizzi et al. 2008), particularly for colonial species who rely on group vigilance to maximize individual survival. Observations from reintroduction experiments of AGS prompted Werner (2015, 2016) to hypothesize that the probability of a dispersing individual successfully settling in a given location will depend on whether that location is already occupied by a minimum number of conspecifics. Without taking these social factors into consideration, population extinction risks could be underestimated or overestimated (Serrano et al. 2001; Serrano and Tella 2003). Although our results show that the presence of conspecifics in the neighborhood helps to explain the AGS occurrence patterns on the landscape, the mechanism behind this pattern is poorly understood. Further research on how metapopulation processes affect dispersal success and colony sustainability is required. Greater emphasis should be placed on investigating the mechanisms driving the clustered distribution of conspecifics within identified habitat. However, because predation appears to be the proximate cause of recent population declines at low elevations (Werner et al. 2016), clarifying how habitat modifies predation success should be a priority in this system. Experimental reintroductions of AGS into a variety of formerly occupied habitats may help answer these questions.

In conclusion, we found that covariates that may deter predation and increase connectivity among colonies within the boreal forest are important factors that appear to determine persistence of remnant populations of AGS at low elevations. Further investigation into predator–prey dynamics and the role of metapopulation dynamics in facilitating successful dispersal in AGS is recommended. A key implication from our study is that shrubification in the boreal forest resulting from climate warming may have reduced visibility, and thus AGS ability to avoid predators, in forested habitats. In Arctic Alaska, AGS also responded negatively to patches with greater shrub height and density (Flower et al. 2019). As such, AGS at low elevations at the southern edge of their range may increasingly rely on areas cleared by humans as their habitat becomes shrubbier. Anthropogenic disturbance may deter predation and enhance AGS habitat to the extent that in some regions, populations largely persist in landscapes with a greater human footprint compared to areas without such disturbance. Recognizing the importance of these habitats in land use planning, and managing potential conflicts with landowners, is likely important for the persistence of AGS at the southern edge of their range.

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