Oecologia (2019) 190:243–254
https://doi.org/10.1007/s00442-019-04400-5

GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Patch use in the arctic ground squirrel: effects of micro-topography and shrub encroachment in the Arctic Circle

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Received: 24 August 2017 / Accepted: 2 April 2019 / Published online: 23 April 2019

Abstract

We investigated the roles of vegetation structure, micro-topographic relief, and predator activity patterns (time of day) on the perception of predatory risk of arctic ground squirrels (*Urocitellus parryii*), an abundant pan-Arctic omnivore, in Arctic Circle tundra on the North Slope of Alaska, where tundra vegetation structure has been predicted to change in response to climate. We quantified foraging intensity by measuring the giving-up densities (GUDs) of the arctic ground squirrels in experimental foraging patches along a heath–graminoid–shrub moist tundra gradient. We hypothesized that foraging intensity of arctic ground squirrels would be greatest and GUDs lowest, where low-stature vegetation or raised micro-topography improves sightlines for predator detection. Furthermore, GUDs should vary with time of day and reflect 24-h cycles of varying predation risk. Foraging intensity varied temporally, being highest in the afternoon and lowest overnight. During the morning, foraging intensity was inversely correlated with the normalized difference vegetation index (NDVI), a proxy for vegetation productivity and cover. Foraging was additionally measured within landscapes of fear, confirming that vegetative and topographic obstructions of sightlines reduces foraging intensity and increases GUDs. We conclude that arctic ground squirrels may affect Arctic Circle vegetation of tundra ecosystems, but these effects will vary spatially and temporally.

Keywords Arctic ground squirrel · Climate change · Giving-up densities · Ecosystem impacts · Foraging · Landscape of fear · NDVI · Tundra

Introduction

Many factors influence predatory risk for prey species, including proximity to cover (Lima 1987; Brown 1988), detectability of predators (Altendorf et al. 2001), illumination (Kotler 1984), escape substrate (Thorson et al. 1998), and habitat heterogeneity or complexity (Crowder and Cooper 1982; Warfe and Barmuta 2004; Chalfoun and Martin 2009). The arctic tundra, characterized by low-stature herbaceous and woody vascular plants, mosses, and lichens (Walker et al. 1994), may be a particularly challenging environment for small vertebrate prey species. The arctic ground squirrel (*Urocitellus parryii plesius*) provides an excellent candidate for investigating the relationship between habitat structure and predatory risk. With a pan-Arctic distribution (occupying areas in eastern Siberia, Alaska and northern Canada), the arctic ground squirrel exhibits high local abundances, stable populations, and great energy demands during the short growing season. In boreal forests below the Arctic Circle, arctic ground squirrels prefer open sight lines in

Communicated by Peter Banks.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00442-019-04400-5) contains supplementary material, which is available to authorized users.

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continuous shrub habitat with high predation risk (Wheeler and Hik 2014). Arctic ground squirrels may become locally extirpated when dense cover prevents predator detection, as shown by Donker and Krebs (2012) in Yukon boreal forest. However, the preference for open sight lines in the arctic ground squirrel in the tundra ecosystem within the Arctic Circle, where taller denser shrubs may be favored by climate change, remains to be documented.

Investigations of the arctic ground squirrel within the arctic tundra have examined diet selection (Batzli and Sobaski 1980; McKendrick et al. 1980), colony structure (Carl 1971), and physiology, particularly with respect to hibernation (Long et al. 2005). Few studies have investigated predation of arctic ground squirrels in tundra habitat since the pioneering work of Carl (1971). Arctic Circle habitats are rapidly changing through a combination of climate and biotic factors (Gough et al. 2012; Leffler et al. 2016; Parmesan and Yohe 2003) which are altering the timing and the interactions between consumers and vegetation (Leffler et al. 2019). As habitat structure is changing rapidly in tundra towards more abundant, taller shrubs (Fung 1997; Myneni et al. 1997; Tape et al. 2006; Myers-Smith et al. 2011; Blanc-Betes et al. 2016), the impact of predation on arctic ground squirrel may also be changing. In this study, we report on experiments that investigated the roles of vegetation structure, micro-topographic relief, and time of day on the perception of predatory risk of arctic ground squirrels in the arctic tundra on the North Slope of Alaska.

Based on studies from the boreal forest and alpine meadows (e.g., Donker and Krebs 2012; Wheeler and Hik 2014; Wheeler et al. 2015), we hypothesized that foraging intensity of arctic ground squirrels from the Arctic Circle would be greatest, where low-stature vegetation or raised micro-topography allows effective sightlines for predator detection. In contrast, foraging intensity would be least in areas of shrub encroachment or low micro-topography (depressions), where sightlines for predator detection are obstructed.

Studies of patterns of below- and above-ground activity documented with light-sensitive radio-collars and implanted temperature-sensitive data loggers (Long et al. 2005) found that arctic ground squirrels typically spent most time underground between 2200 and 0500 h, with most surface activity occurring between 0500 and 2200 h (with exceptions owing to daily variation in temperature and precipitation). The percentage of time spent on the surface tended to increase during the morning until the midday, and then decrease as the afternoon progressed. Long et al. (2005) attributed these daily activity patterns to thermal and non-thermal variables that minimize thermoregulatory and activity costs. While acknowledging a potential role for predator presence to affect patterns of surface activities, they were unable to include this factor in their analyses. We hypothesized that predator activity patterns strongly affect surface activity patterns of Arctic ground squirrel, and we expected that foraging intensity will be least when predator activity is greatest. To test this, we measured foraging intensity over three equal-length time periods of 24 h day that correspond to known patterns of surface activity of the arctic ground squirrel along vegetation structure, height and biomass gradient.

Materials and methods

Study site

The study was conducted in late July and early August 2014, and early July through early August 2015 at the Toolik Field Station, in the foothills of the Brooks Range on Alaska's North Slope (68°38′N, 149°36W elevation 760 m a.s.l.). The study site consisted predominantly of gradients of dry heath tundra to moist tussock tundra ecotones. Briefly, vegetation consisted of non-tussock-forming sedges and grasses, tussock-forming graminoids (*Eriophorum vaginatum*), intermixed with low stature and canopy-forming willow and birch species (*Salix pulchra*, *S. alaxensis*, and *Betula nana*). Topographical strata range from elevated granite substrates to low-lying floodplain. The study was restricted to a roughly 10 ha area west of the NSF ITEX (International Tundra Experiment) dry heath fence within which we identified at least 4 independent colonies of squirrels. All Arctic ground squirrel burrows within the study area were identified and mapped via GPS (Trimble Inc., Sunnyvale, CA). All data generated or analyzed during this study are included in this published article and supplemental materials.

Arctic ground squirrels are widespread semi-fossorial rodents inhabiting Arctic tundra, alpine meadow and boreal forest (Hall 1981). For burrowing, they prefer sloped terrain with adequate drainage, permafrost layer below 1 m or more in depth, and sparse vegetation. As an obligate hibernator, they are active for only 3–5 months of the year, emerging as early as mid-April and remaining active as late as September (Buck and Barnes 1999). Arctic ground squirrels are opportunistic foragers with a broad diet consisting of plants, fungi, invertebrates, and occasionally small vertebrates. Squirrel home ranges vary between 1400 and 21,800 m^2 (Carl 1971; Barker and Derocher 2010), yet the majority of foraging typically occurs within 30 m from burrows (Batzli and Sobaski 1980). Diet preference has been documented via caching behavior, stomach contents (Gillis et al. 2005; Zazula et al. 2006), and palatability trials, showing a preference for forbs and deciduous shrubs (*Salix* spp.) with high water content. Forbs and grasses account for 20–75% of their overall diet (Batzli and Sobaski 1980). Preferred burrowing habitat includes open and elevated areas with little to no vegetation (Karels and Boonstra 1999; Barker and Derocher 2010). Because foraging intensity varies during the growing

season, the experiments were carried out during the post-breeding season in late July and early August, when individuals must gain weight and accumulate fat to survive their long hibernation.

Canopy spectral imaging (NDVI) and shrub biomass and height

Throughout the paper, we use normalized difference vegetation index (NDVI; a proxy of vegetation greenness) as a proxy for vegetation standing crop structure (biomass and height). We quantified vegetation greenness along six study transects set up to study Arctic ground squirrel foraging (see below) with a dual channel portable spectroradiometer (Unispec-DC, PP Systems International, Inc., Amesbury, MA) that simultaneously measured plot radiance and sky irradiance. The resulting NDVI of each 1 m^2 foraging area (foraging tray excluded during measurement) was measured using average reflectance in the red and near infrared spectral regions as described by Anderson-Smith (2013). Although the relationships between NDVI and green biomass of heath and moist tundra are well established (Hope et al. 1993), we conducted our own determinations of NDVI with total biomass, height, and productivity on random plots in tundra near our transect areas at Toolik Lake. To determine the relationship between NDVI and plant biomass, we quantified above-ground vegetation biomass (g m^{-2}), vegetation height (cm), and NDVI within 20 70 cm^2 quadrats located randomly in dry heath, moist non-acidic, and moist acidic tundra. These quadrats were located away from the site of the foraging experiment to avoid interference but on the same tundra and soil types as in the foraging transects using the land cover map available at the LTER Toolik field station website. Average vegetation height was determined by summing the maximum height of each shrub within each quadrat and dividing by the number of shrubs. Above-ground shrub biomass was destructively harvested within each quadrat and oven-dried until constant dry weight. We then regressed the $\log_{10}$ transformed plant biomass against NDVI (14 plots) and the $\log_{10}$ transformed vegetation height against the $\log_{10}$ transformed above-ground shrub biomass (12 plots).

Foraging along gradients of vegetation density and height

We measured foraging intensity with giving-up densities (GUDs) in experimental food patches (Brown 1988; Brown and Kotler 2004) deployed in a nested block design with six transects of 5 foraging stations each. Within each transect, the five stations traversed a microhabitat gradient beginning in sparsely vegetated dry heath tundra (stations 1 and 2), moving into moist acidic tundra (stations 3 and 4), and culminating in densely shrub-covered tundra (emulating predicted future shrub encroachment scenarios; station 5). Stations with similar numbers are, therefore, placed within a similar cover type within each transect regardless of distance between stations. Stations were between 5 and 8 m apart. Transects were ~ 30 m long to assure that all five foraging stations were accessible to the same squirrel or group of squirrels. Transects were > 50 m apart and collectively encompassed at least four clearly identifiable independent colonies. Each transect was situated, so that the first station (station 1) was no more than 2–3 m from an active burrow.

Experimental food patch

Over a period of 10 days in late July 2014, we optimized the foraging patch tray design, which consisted of circular plastic trays (36 cm diameter/5 cm deep) filled with 1.5 L pea gravel, with small drain holes (Fig. 1). We used 20 raw peanut halves and 20 raisins per tray, with two whole peanuts placed on top to serve as initial bait. Though novel to the squirrels, we intentionally used peanuts and raisins. They represent both hard and soft food textures that are present in the tundra habitats. To create diminishing returns to foraging in the patches, we inserted a plastic mesh disc (5 cm mesh) that rested on and covered the gravel. To keep the mesh in place, we attached a 2 × 2 grid of heavy gauge wire placed 9 cm apart through holes drilled in the upper lip of the trays. GUDs were measured

Fig. 1 Arctic ground squirrel at a 2014 experimental foraging patch. In this design, a circular plastic tray (36 cm diameter/5 cm deep) was filled with 1.5 L pea gravel, with small drain holes. Patches were baited with 20 raw peanut halves and 20 raisins per tray, with two whole peanuts placed on top to serve as initial bait. To create diminishing returns to foraging in the patches, we inserted a plastic mesh disc (5 cm mesh) that rested on and covered the gravel. To keep the mesh in place, we attached a 2 × 2 grid of heavy gauge wire placed 9 cm apart through holes drilled in the upper lip of the trays

by counting the number of remaining peanuts and raisins in the tray after a feeding period. The chosen food items are particulate, providing uniform and repeatable quality, resistant to the weather, readily recognized as food to the squirrels, and the two together allowed for higher resolution of foraging behavior and GUD quantification (see Bedoya-Perez et al. 2013; Kotler et al. 2016). Being preferred, peanuts were sometimes foraged to zero, and, being less preferred, raisins at times were skipped even as peanuts were consumed. Together, the combined GUD on the peanuts and raisins in a food patch gave us wider spectrum over which to measure foraging efforts and costs.

In 2015, during pre-bait trials using the 2014 foraging tray design, squirrels totally depleted the patches. Therefore, to assure diminishing returns during food depletion, a second plastic mesh disc and 10 roughly 5 cm rocks were inserted in each tray. This increased the level of difficulty for the squirrels to deplete the patch, insuring non-zero GUDs. The different patch designs mean that GUDs from 2014 and 2015 are qualitatively but not quantitatively comparable. Moreover, a given GUD in 2014 represents less effort than the same GUD in 2015.

Giving-up density (GUD)

We measured foraging intensity (the GUD) in the experimental foraging patches in three equal-length time periods (05.00–13.00, 13.00–21.00, and 21.00–05.00) over the 24 h daily cycle based on reported activity periods for the arctic ground squirrel (Long et al. 2005). These equal-length time periods were chosen to reflect daily shifts in below- and above-ground activity patterns of arctic ground squirrels previously documented with light-sensitive radio-collars and implanted temperature-sensitive data loggers (Long et al. 2005). We refer to foraging trials conducted during each of the three equal-length time periods on subsequent days as "runs."

Our food patches produced diminishing returns for the squirrels, as they harvest the resources. Consequently, the forager's harvest rate declines, as the patch is depleted, and eventually, it abandons the patch (Brown 1988). The forager should abandon the patch when its harvest rate no longer exceeds the sum of its metabolic, predation and missed opportunity costs of foraging. The food remaining in the patch after the foraging round constitutes the GUD. During each round of data collection, gravel was poured from the trays into a larger plastic saucer, the remaining peanut halves and raisins were removed and counted, and the trays were refilled with a fresh aliquot of 20 peanut halves, 20 raisins, and two indicator peanuts. The GUDs represented the sum of the peanuts halves and raisins left in the tray.

Photographs

A motion-sensitive camera trap (Moultrie® Game Spy D-40 4.0 Megapixel Digital Game Camera), equipped with a 1 or 2 GB sd card and deployed at stations 1 and 3 of each transect (for a total of 12 cameras), monitored foraging activity and species' identities. Each camera trap was set to take three high quality still photographs in succession upon triggering to ensure the animal was photographed. Latency between triggering events was set at 1 min, and each camera was set to use its built-in flash when the light level required it. Animals in only one of the triplet photographs were counted to avoid counting the same individual multiple times. We noted evidence of sporadic vole activity (e.g., tunnels) and foraging at two stations, each in a different transect. After noting evidence of voles at station 5 of transect 6 during the fourth run, the camera was moved from station 3 to station 5 to confirm vole activity. Evidence of vole activity/foraging was also noted at station 5 of transect 5 later in the experiment, but the camera was not moved. No evidence of vole activity/foraging appeared at the other transects or at other stations of transects 5 and 6. The photo frames were analyzed for all visitors, which included herbivores besides arctic ground squirrels and predators.

Landscape of fear (LOF)

To determine whether predation risk varies within the home range of a squirrel, and to relate the squirrels' fear of predation to sightlines and/or vegetation cover, in 2014, we haphazardly located a 4 × 4 grid of food patches (16 trays total) with 10 m spacing between patches within an established arctic ground squirrel colony. Patches used for the LOF were identical to those used in the transect study. The entire grid was in dry heath tundra habitat with heterogeneous topography of small rises and depressions, although topography generally rose from the NE corner toward the SW corner. Data were collected five times over a 4-day period. In addition, photos were taken at each foraging patch in each of the four cardinal directions at a height of approximately 17 cm to simulate the sightline height of a squirrel standing vigilant. Photos were additionally taken from overhead to document evidence of vertical obstruction. Each photo was given a value for vegetation (0 = 0–33% lateral obstruction, 1 = 34–66% lateral obstruction, and 2 = 67–100% lateral obstruction), slope (0 = none, 1 = partial, and 2 = total), and overhead obstruction (0 = none, 1 = some). Scores were assessed and assigned by four independent observers. Using GPS, we recorded the latitude and longitude of all foraging patches and mapped all the burrow entrances on and within 10 m of the grid, noting that squirrels tended to reside on the NW corner and along the northern margin of the grid.

In 2015, we measured LOFs at three new sites, each with at least one arctic ground squirrel colony. Each site (block) was a 3 × 3 grid of food patches (27 feeding patches total). Each feeding patch was placed 10 m apart within each block. The three blocks were more than 150 m from one another to ensure no or little overlap in use by squirrels. The site of each block was chosen to resemble the 2014 LOF with a heterogeneous landscape of undulating topography and variable vegetation. GUDs were collected twice a day (0500–1300, 1300–2100) over a 2.5-day period for a total of 5 runs. Logistical constraints prohibited the collection of photos to analyze local obstructions as was done in 2014. Therefore, each station was scored on a scale of 1–3 with respect to vegetation cover (3 representing high vegetation and obstructed sightlines), and 1–3 with respect to whether the food patch was elevated or within a depression (3 representing high elevation and unobstructed sightlines).

Potential predators of Arctic ground squirrels

At Toolik Lake, of 6 potential mammalian predators, only the red fox (*Vulpes vulpes*) frequently occurs at the station. Gray wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*), known predators of arctic ground squirrels (Barker et al. 2015) are rarely seen near the station. Mammal data were obtained from the Toolik Lake Field Station Environmental Data Center (http://toolik.alaska.edu/edc/biotic/monitoring/mammal_guide.php).

A variety of potential avian predator species (8 raptors, 3 owls, 1 gull, 1 jaeger, and 1 corvid) inhabit the North Slope of Alaska. At Toolik, jaegers (*Stercorarius longicaudus*) were often seen during the study but they prey primarily on voles (Carl 1971). The common raven was observed daily (and l photos were obtained at foraging patches, see below), but they appear to be competitors rather than predators of arctic ground squirrels at Toolik. Golden eagles (*Aquila chrysaetos*) are rarely seen hunting over the Toolik area, but none was observed during our study. Snowy owls (*Bubo scandiacus*) are found more commonly on the coastal plains away from Toolik, and none were observed during our study. Bird observational data were obtained from the Toolik Lake Field Station Environmental Data Center (http://toolik.alaska.edu/edc/biotic_monitoring/bird_guide.php).

Growing degree days

Because we conducted the experiments over two consecutive years with different weather patterns that can affect productivity (Partain et al. 2016) and, therefore, foraging behavior, we calculated growing degree days to compare both years. Results are presented in the supplemental materials. Growing degree days are an index of heat accumulation during the growing season, and they are useful for predicting plant and insect development or emergence (Anandhi 2016).

Statistical analyses

Foraging along gradients of vegetation density and height

To examine differences in foraging intensity within and among transects, we tested for differences among GUDs with a partially hierarchical ANOVA with time period (05.00–13.00; 13.00–21.00; 21.00–05.00) and transect (6) as group variables, 8-h runs (12) nested within time periods, stations (30) nested within transects, and the interaction effect between time periods and transect. We summed the total remaining peanuts and raisins (the GUD) and then square root transformed that sum to achieve assumptions of normality. We tested for differences in mean NDVI among the six transects with a one-way ANOVA. To investigate a potential relationship between foraging intensity and vegetation density, we regressed mean total GUDs of a station ($n = 30$) against the station's NDVI score at each station. We ran a separate regression for each foraging period.

To examine the potential role of weather (temperature, precipitation, and humidity) on foraging intensity, we used an ANCOVA with mean GUD for a run as the dependent variable, time period as a grouping variable, and temperature, precipitation, and relative humidity during the run as covariates.

Landscapes of fear

In 2014, we tested for differences in GUDs (square root of total GUD, raisins plus peanuts) across the 4 × 4 grid with a two-way ANOVA using station and run as independent variables. To determine effects of topography and vegetation across the LOF grid, we regressed (multiple regression) the mean GUD of a station against its vegetation score, sightline score, and their interaction. Because the interaction term was not significant, ($t = 0.59$, $P > 0.5$), we then ran the multiple regression omitting the interaction term to test for differences in intercepts.

In 2015, we tested for differences in GUDs within and among the three 3 × 3 grids (main effect of site). In a partially hierarchical ANOVA, the dependent variable was the square root of total GUD, site and run (5 8-h foraging periods over 2.5 days) were group variables (including their interaction effect), and station nested within site was the error term to test for the significance of site. To explore how the variability of vegetation and topography across stations nested within site may have affected GUDs, we conducted an ANCOVA with site as a grouping variable, and vegetation and sightline as covariates (having first found no significant interaction of site with either vegetation or with sightline).

The mean quitting harvest rates at all food patch positions within each of the 2014 and 2015 LOF sites were mapped and then contoured with the Spatial Statistics procedure in Systat13 (SYSTAT Version 13). Points were interpolated using a spline curve, which fits a minimum-curvature surface through all input points. Mean quitting harvest rates were represented as contour lines.

Results

Canopy spectral imaging (NDVI) and shrub biomass and height

Mean NDVI did not differ among six transects ($F_{5,24}=1.43$, $P=0.249$). Overall mean NDVI was 0.702 ± 0.035 (range of 0.479–0.865). With linear regression, we found positive relationships between NDVI and plant biomass (g m^{-2}): $\log_{10}(\text{biomass}) = 5.79 \times \text{NDVI} - 1.74$ ($P<0.001$, $R^2=0.715$; Fig. 2a), and between plant biomass (g m^{-2}) and plant height (cm): $\log_{10}(\text{plant height}) = 0.466 \times \text{Biomass} + 0.449$ ($P=0.002$, $R^2=0.613$; Fig. 2b).

Foraging along gradients of vegetation density and height

The overall ANOVA model provided a good fit to the data (multiple $R^2=0.755$). Giving-up densities differed significantly with time period, with the lowest GUDs occurring during the afternoon (13.00–21.00) and, the highest during the night (21.00–05.00; $F_{2,9}=12.01$, $P=0.003$; Fig. 3a). The GUDs did not differ significantly among transects ($F_{5,24}=2.25$, $P>0.08$) indicating similar patterns of foraging intensity across the different squirrel home ranges. A significant interaction between time period and transect reflected a tendency for squirrels to skip some transects altogether during different time periods ($F_{10,309}=10.87$, $P<0.001$). As random effects, GUDs varied significantly with both stations within transects ($F_{24,309}=2.60$, $P<0.001$) and runs within time periods ($F_{9,309}=22.81$, $P<0.001$).

GUDs varied positively with NDVI during the morning period ($F_{1,28}=17.01$; $P<0.001$; $R^2=0.378$), but showed no relationship during the afternoon ($F_{1,28}=0.349$; $P=0.559$) when foraging intensity was consistently high (low GUD), nor during the overnight period ($F_{1,28}=0.6329$; $P=0.433$) when foraging intensity was consistently low (high GUD; Fig. 3b).

GUDs exhibited no relationship with air temperature (ANCOVA, $F_{1,66}=0.29$, $P=0.588$), precipitation (ANCOVA, $F_{1,66}=0.04$, $P=0.842$), or relative humidity (ANCOVA, $F_{1,66}=0.29$, $P=0.587$).

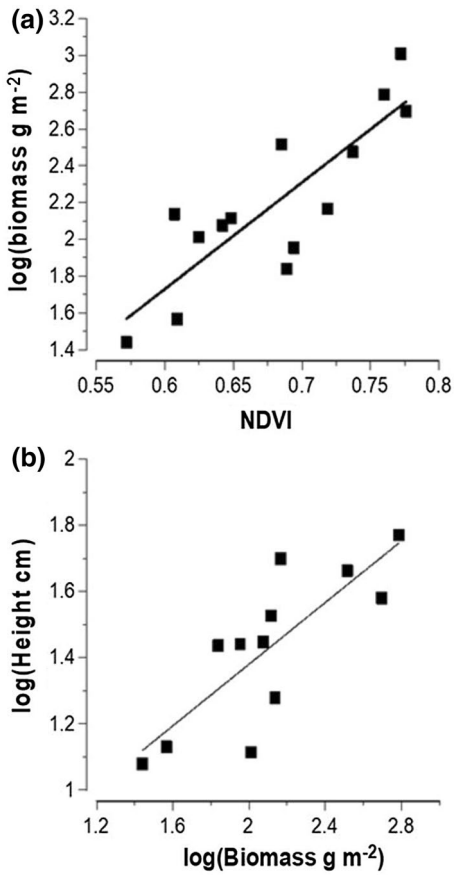

Fig. 2 Relationships among NDVI, vegetation biomass (g m^{-2}), and vegetation height (cm). **a** Linear relationship between NDVI and $\log_{10}$(vegetation biomass): $\log_{10}(\text{biomass}) = 5.79 \times \text{NDVI} - 1.74$, $P<0.001$, $R^2=0.715$. **b** Linear relationship between vegetation biomass (g m^{-2}) and vegetation height (cm): $\log_{10}(\text{plant height}) = 0.466 \times \text{Biomass} + 0.449$, $P=0.002$, $R^2=0.613$

Photographs

The 12 motion-triggered cameras photographed a total of 811 images with animals present at experimental food patches. Species photographed included Arctic ground squirrel (83%), vole (7.3%), raven (5.2%), fox (3.2%), and sparrow (1.3%; see Table 1). Foxes were photographed predominantly during the overnight period (Table 1) when GUDs were greatest (Fig. 4a). Voles were photographed only at station 5 of transect 6, yet accounted for 7.3% of all photographs. Voles were photographed most frequently during the morning period (87%). Visits to foraging trays (indexed by photographs) were dominated by squirrels in the morning (79%) and afternoon (93%), the periods of lowest GUDs. It is important to note that vole photos were inflated by our decision to move a camera to the place, where we discerned the most evidence of voles. Squirrels were photographed significantly more frequently at station 1 (closest to burrows) than station 3 (Welch's T test, $t_{7.13}=2.62$,

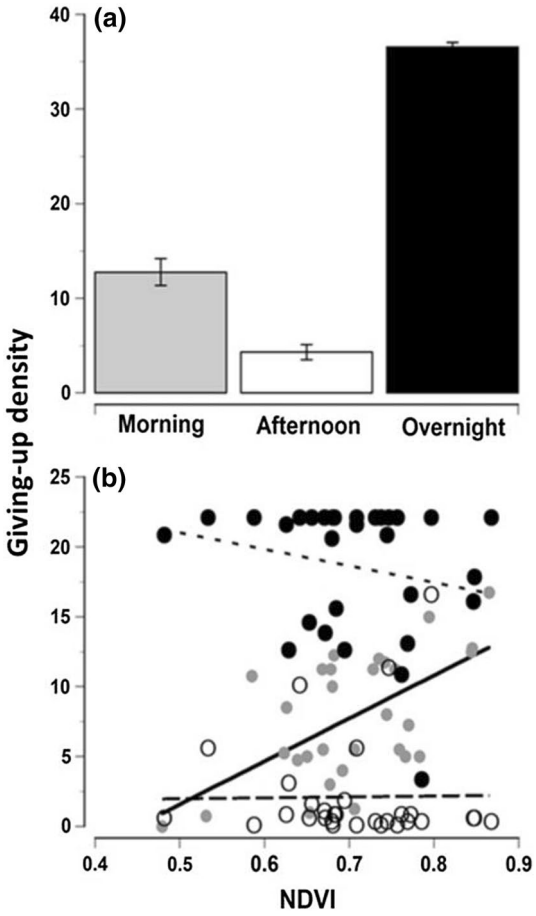

Fig. 3 **a** Back-transformed mean (±1 standard error) giving-up density (GUD) for each foraging period. Each foraging period differs significantly from all other (Tukey's HSD pairwise comparisons; $P<0.05$). **b** Linear regressions between normalized differential vegetation index (NDVI) and giving-up densities at each foraging station during three foraging periods. Shading matches panel (**a**), with morning, afternoon and overnight represented by gray, white and black circles, respectively. The solid line corresponds to the morning period, the dashed line corresponds to the afternoon period, and the dotted line corresponds to the overnight period

$P=0.034$; Fig. 4a), and squirrels were photographed most frequently during the morning and afternoon periods, and least overnight (Fig. 4b).

In evaluating the other species (14% of the photographs), there was no photographic evidence of foxes, a major predation risk factor for arctic ground squirrels, foraging from the patches. A female fox who was raising her young under some buildings of the field station was routinely seen returning with captured arctic ground squirrels (our observations and others' personal communication). The ravens and sparrows may have been able to take the two peanut halves on the surface occasionally, but there was no photographic evidence of birds attempting to forage through the pea gravel. Ravens may represent a harassment cost to arctic ground squirrels and may contribute to the squirrel's higher GUDs in the morning than afternoon.

Landscape of fear

In 2014, GUDs varied significantly with both run and station ($F_{4,60}=17.614$; $P<0.001$ and $F_{15,60}=3.235$; $P=0.001$, respectively; Figs. 5, 6). The model provided a good fit to the data (multiple $R^2=0.665$). GUDs increased with vegetation cover ($t=2.86$, $P=0.013$), and decreased non-significantly with sightline obstruction ($t=1.7$, $P=0.11$). The relationship was mean GUD at a station $=7.1-1.15\times$Sightline $+1.18\times$Vegetation.

In 2015, GUDs differed significantly among the sites ($F_{2,24}=10.88$, $P<0.001$; Fig. 6). GUDs did not differ with run period ($F_{4,24}=1.43$, $P=0.228$), though there was a significant interaction of run and site ($F_{8,96}=5.28$, $P<0.001$). Finally, GUDs varied significantly across stations nested within sites ($F_{24,96}=1.64$, $P=0.047$; Fig. 6b, c). The overall model provided a moderately good fit to the data (multiple $R^2=0.562$). GUDs varied significantly among the three sites (ANCOVA, $F_{2,47}=5.35$, $P=0.008$) and with sightlines (ANCOVA, $F_{2,47}=4.78$, $P=0.013$) but not with vegetation (ANCOVA, $F_{2,47}=0.33$, $P>0.7$).

In the context of these results, it is important to note that the beginning of the 2015 growing season was warmer and earlier by 14 days than in 2014 (Supplemental Fig. 1). Growing degree days rose faster in 2015 than 2014 (two sample Kolmogorov–Smirnov test, $P=0.069$; Anderson–Darling test, $P=0.04$). Regardless, 2 years of data support the

Table 1 Number and proportion of photographs of different animals present at experimental food patches contingent upon time of day

	Morning (number)	Morning (%)	Afternoon (number)	Afternoon (%)	Overnight (number)	Overnight (%)	Total (%)
Fox	5	1.2	3	0.8	18	43.9	3.2
Raven	25	6.0	17	4.8	0	0.0	5.2
Sparrow	7	1.7	3	0.8	1	2.4	1.3
Squirrel	328	78.8	329	92.9	16	39.0	83
Vole	51	12.3	2	0.6	6	14.6	7.3
Total	416		354		41		

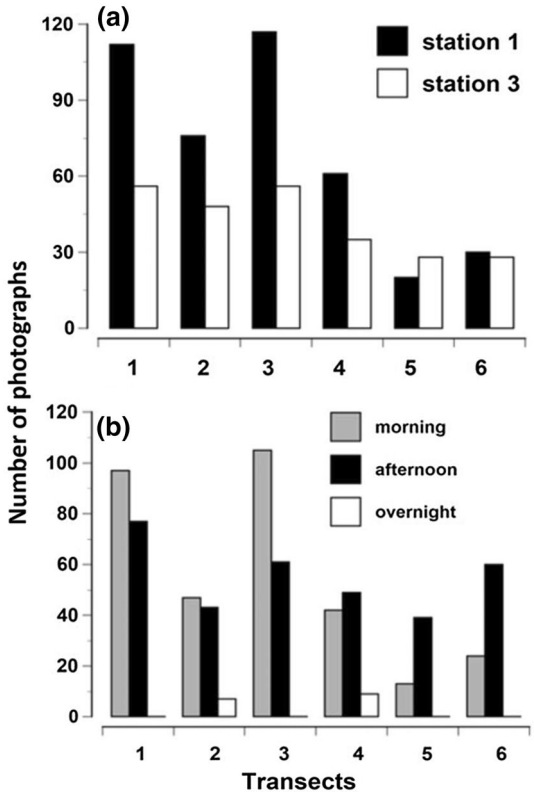

Fig. 4 **a** Number of photographs with Arctic ground squirrels at stations 1 and 3 by transect. Some station three photographs of transect 6 include photographs taken at station 5 after the camera was moved to confirm vole foraging (see "Methods"). **b** Number of photographs of Arctic ground squirrels per transect subdivided by time of day (morning, afternoon, and overnight)

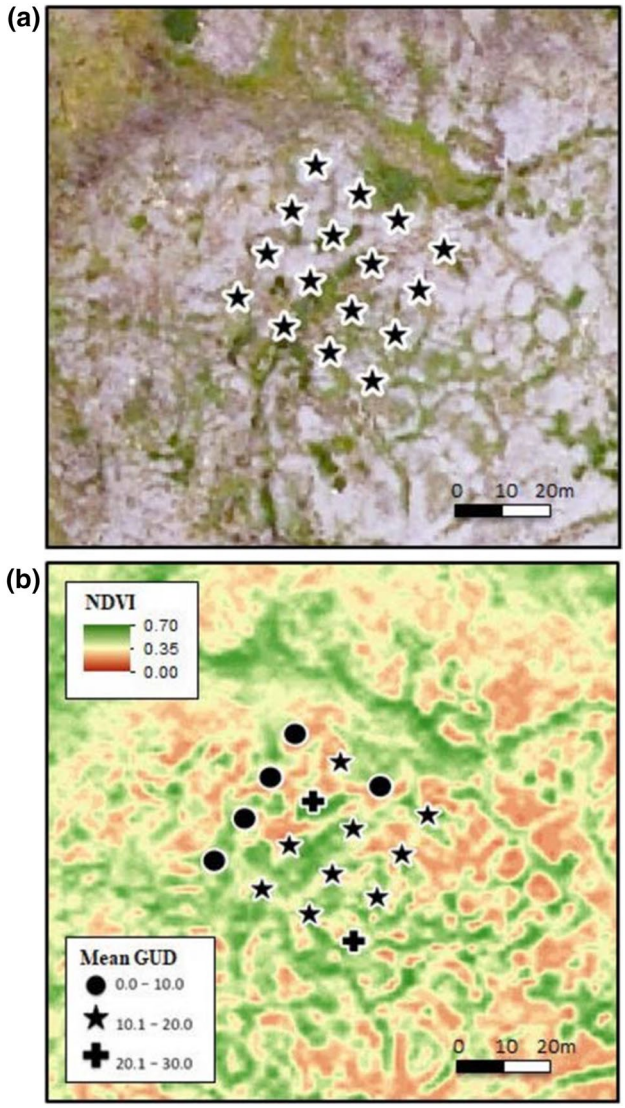

Fig. 5 Two representations of the 2014 landscape of fear (LOF). **a** True color Orthomap (60 cm resolution) with stations depicted with stars. Stations are 10 m apart. *Image courtesy of Toolik Field Station GIS.* **b** NDVI map (0.3 m resolution) with mean GUD values at each station classified as high risk (cross), moderate risk (star), or low risk (circle). *Image courtesy of the DigitalGlobe Foundation*

conclusion that GUDs decrease with sightlines and increase with vegetation.

Discussion

Arctic ground squirrel foraging intensity varied spatially. Close to tall and dense shrubs (high NDVI) and in topographic depressions, arctic ground squirrel foraging was cursory or superficial (high GUDs; Figs. 3b, 6a). In areas of sparse vegetation (low NDVI) and topographic ridges and mounds, foraging patches were depleted more thoroughly (low GUDs; Figs. 3b, 5b). Our results from Arctic Circle tundra are consistent with those from studies of arctic ground squirrels at lower latitudes in alpine meadows and boreal forest (Wheeler and Hik 2014; Wheeler et al. 2015; Donker and Krebs 2012). Arctic ground squirrels forage food patches more thoroughly, where they have good sightlines and/or low vegetation cover, and much less thoroughly when sightlines are poor and vegetation dense. Owing to their widespread distribution and high abundances throughout the Arctic of North America and Siberia (Hall 1981), we hypothesize that arctic ground squirrel could exert ecosystem-level effects on tundra vegetation composition and structure, and such effects will be spatially heterogeneous.

In addition to spatial variability, arctic ground squirrel foraging intensity varied by time of day (Fig. 3b). In the morning period, foraging intensity varied inversely with NDVI, with low GUDs associated with sparse vegetation (low NDVI), and high GUDs associated with tall and dense vegetation (high NDVI; see Fig. 2). We hypothesized that the sensitivity of arctic ground squirrel foraging intensity to vegetation mass and height during the morning bout (Fig. 3b)

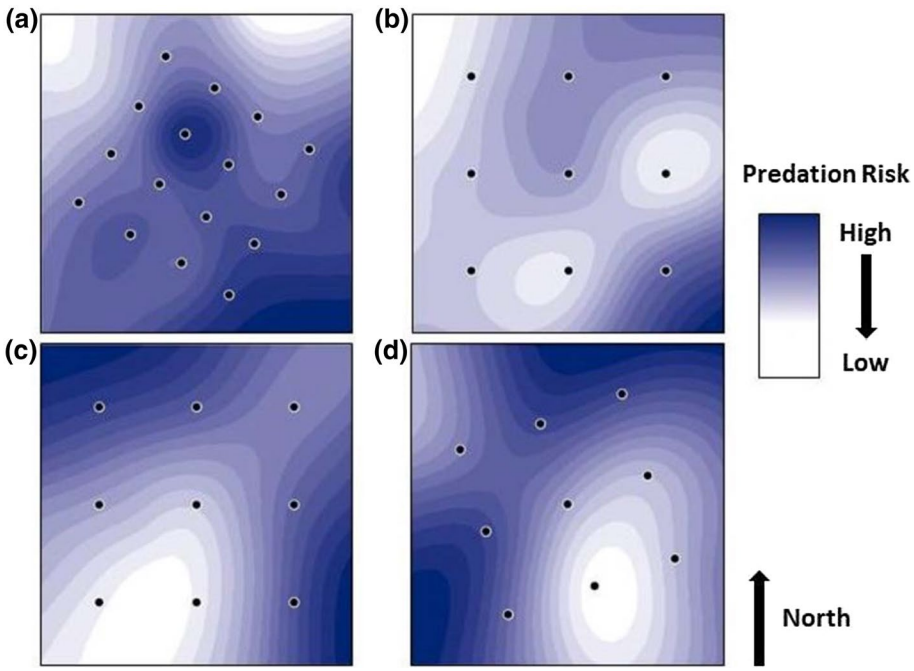

Fig. 6 "Heat maps" of 2014 and 2015 landscapes of fear (LOF). Colors represent gradients of perceived predation risk based on giving-up densities, with white representing least risk and darkest blue representing greatest risk. **a** 2014 4×4 LOF grid. 10 m spacing; **b**–**d** the three 3×3 grid LOFs in 2015, 10 m spacing

reflects carryover predation effects from the overnight period, when red foxes are most active (Table 1). During the morning, therefore, Arctic ground squirrels forage intensely in areas of low-risk areas in which low NDVI affords good sightlines for predator detection. Foraging in early-to-late afternoon was uniformly intense. This is a period when light levels are high, red foxes are relatively inactive (based on camera traps), and thermoregulatory costs are minimal (Williams et al. 2014). Foraging during the overnight period, when red foxes are most active (Table 1), was uniformly light irrespective of habitat and features (high GUDs). Thus, the morning period of moderate predation risk accentuated the effects of cover and sightlines on GUDs.

Based on differences in GUDs, the effects of predation risk were scale dependent. Over 2 years we examined: (1) station-to-station variation in risk (5–8 m spacing of trays along transects); (2) variation in risk as an LOF within an area of c. 0.1 ha (4×4 grid of patches with 10 m spacing in 2014); and (3) differences in perceived risk among sites (three LOF sites of 2015, separated by roughly 0.15 km). We found significant effects at all three scales. At the scale of a station, predation risk is a composite of predator visitation rates (camera trap data), sightlines, topography, and NDVI. At the site scale, variation in the presence and visitation rates of predators, in combination with variation in sightlines, vegetation, escape routes, and burrows, promotes landscape-scale variation in squirrel foraging intensity.

Weather and plant-growing conditions varied markedly between 2014 and 2015 with the growing season of 2015 being warmer and drier across Alaska (Supplemental Fig. 1; Partain et al. 2016). Variation in summer climate at high latitudes affects the onset time and the length of the growing season for vegetation affecting its phenology and availability of food items (Parmesan and Yohe 2003; Leffler et al. 2016; Bjorkman et al. 2015). As such, inter annual weather variations have been shown to affect population dynamics and behaviors of food-limited vertebrates (Albon et al. 2017; Boelman et al. 2017). The varying results of vegetation and sightline effects between the 2014 and the 2015 LOFs may reflect the difference in plant-growing conditions and their productivity (see GDD supplemental Fig 1; Blanc-Betes et al. 2016). Regardless of weather conditions, in both years, sightlines were important determinants of fear. In 2014 sightline, obstruction was caused primarily by vegetation, whereas in 2015, sightline obstruction resulted primarily from topographic heterogeneity, which may act in concert with vegetation height to influence fear.

The landscape of fear of the arctic ground squirrel is not unique as sightlines impact predation risk in other relatively low productivity ecosystems. For instance, the Cape ground squirrel (*Xerus inauris*), measured in the Karoo Desert, South Africa (van der Merwe and Brown 2008) showed high GUDs near vegetation and blocked sightlines and low GUDs near burrows and in open areas. Both ground squirrels could see large changes in predatory risk within a few meters. In contrast, work with the closely related African unstriped squirrel (*X. inauris*) reveals the necessity of evaluating a species-specific LOF. In the desert scrub habitat of Tsavo West National Park, Kenya, this squirrel showed no difference in GUDs between open and bush microhabitats, except in rocky habitats, where the bush microhabitat was greatly favored over the open,

as measured by GUDs (Fanson et al. 2010). Other animals showing landscapes of fear, where sightlines and openness had lower GUDs and lower perceived predation risk include goats (Shrader et al. 2008), springbok (Kotler et al. 2016), and mountain nyala (Tadesse and Kotler 2013). The landscape of fear of Nubian ibex (*Capra nubiana*; Iribarren and Kotler 2012) showed opposite effects, where vegetation increases perceived predation risk. There is growing interest in LOFs in species interactions such as trophic cascades and as mechanisms of coexistence (Laundré et al. 2014). Our study complements and adds to this literature.

A key consideration in all such LOF studies is the distance between sampling points (stations). Place stations too close together and there may be little to no change in predation risk. Place stations too far apart, and there may not be a monotonic gradient in fear between adjacent stations, but rather one of more ups and downs that would be missed. For instance, stations needed to be no more than 3 m apart to reveal the highly rugose LOF of Namaqua mice (*Micaelamys namaquensis*) inhabiting a very heterogeneous rocky environment (Abu Baker and Brown 2012). The dry heathland of the arctic ground squirrel does not appear that heterogeneous and 10 m spacing between stations seemed adequate for capturing vegetation and topographic features of importance to the ground squirrels. As in other measures of LOFs, our work demonstrates LOFs will have unique scale dependencies based upon the characteristics of the forager and properties of the landscape.

We propose by way of hypothesis based on the LOF of the arctic ground squirrel (Fig. 5) that where they feel safe, they may forestall shrub encroachment, and where they feel fearful they may have little to no effect on shrub encroachment. In addition to climate, consumer-driven interactions may drive changes in composition, structure, and productivity of ecosystems (Flower and Gonzalez-Meler 2015; Flower et al. 2013) including those in the Arctic habitats (McKendrick et al. 1980; Gough et al. 2012; Leffler et al. 2019). Overall, the predicted shrub expansion in areas of the Arctic Circle will likely alter the landscape of fear for the arctic ground squirrel. Expanding fear effects may limit areas in which arctic ground squirrels may forage effectively for the resources needed for sustaining populations. Ultimately, shrub expansion may limit the viability of the arctic ground squirrel over large areas of tundra, as has already been observed in boreal forest to the south (Donker and Krebs 2012). At the landscape scale, however, arctic ground squirrels are associated with tundra areas with limited shrub cover in the boreal-tundra transition ecotones (Barker and Derocher 2010). Our results invite further attention to the likely complex interactions between arctic ground squirrels and the composition of vegetation in the Arctic.

Conclusions and future directions

We found that foraging intensity of arctic ground squirrels is strongly affected by variation in micro-topographic relief in combination with variation in vegetation height and density and diel cycles. Environmental effects were contingent upon time of day, being most pronounced in the early hours of the day (despite the 24 h light cycle during our study) because of carryover effects from the previous night when activity of the red fox was greatest. Our results imply a feedback between the arctic ground squirrel, spatial patterns of vegetation, and temporal patterns of predator activity. Our approach, combining measurements of GUDs along transects through gradients of existing vegetation structure and NDVI values, coupled with the landscapes of fear experiments, demonstrates an effective conceptual and methodological approach for dissecting the interactive effects of micro-topographic relief and heterogeneity in vegetation heights and densities on the perception of fear of an important and widespread herbivore. Our combination of foraging theory, landscape features, and trophic interactions provides a broadly applicable means for integrative, scale-dependent studies of top–down and bottom–up ecosystem effects.

Acknowledgements This research was supported by the US Department of Energy, Terrestrial Ecosystem Science Program (DE-SC 0006607 to MAG-M), a grant by the College of Liberal Arts and Sciences (MAG-M), the Stable Isotope Laboratory at the Department of Biological Sciences at UIC, and the International Tundra Experiment (ITEX). The authors thank N. van Hoey, J.M. Welker, and M. Anderson-Smith for support with NDVI measurements, staff at NSF LTER/Toolik Field Station and GIS Office (R. Fulweber). E. Blanc-Betes and M. Ricketts provided useful feedback during the experimentation and data analyses. A. H. Halloway kindly assisted with data analysis. Weather datasets were provided by the Toolik Field Station Environmental Data Center. JED thanks the Grant-in-Aid of Research support from the American Society of Mammalogists, and the Department of Biological Sciences and the College of Liberal Arts and Sciences at the University of Illinois at Chicago for providing additional support. CEF recognizes the USDA Forest Service Northern Research Station for helping to support his travel in 2014.

Author contribution statement All authors contributed to the final version of the manuscript. Author contributions: All authors shared equally with the conception and execution of the experiment. JSB, CJW, and CEF conducted the statistical analyses.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest in the authorship of this article.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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