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SIBERIAN MARMOT *(MARMOTA SIBIRICA)* ECOSYSTEM ENGINEERING SUPPORTS DARKLING BEETLES *(BLAPS RUGOSA)* IN HUSTAI NATIONAL PARK, MONGOLIA

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Ecosystem engineering – the physical modification of habitat by a species - can create habitat patches that affect the distribution and abundance of other species relative to adjacent, unmodified habitats. The Siberian marmot *(Marmota sibirica)* is a large, endangered rodent that lives colonially and creates extensive burrow systems that change the soil nutrient profile and influence plant and animal community composition and productivity. The effect of marmot burrows on invertebrates remains largely unexplored, yet may have conservation implications for species that perform various ecosystem services. Here we surveyed the occupancy of darkling beetles *(Blaps rugosa)*, a common invertebrate in forest-steppe ecosystems, in relation to marmot burrow colonies and other landscape variables in Hustai National Park, Mongolia. We surveyed 130 sites, including 43 active burrow sites, 45 non-active burrow sites, and 42 control sites with no burrows in the summer of 2016 and used a model selection approach to develop an occupancy model for the species that accounted for imperfect detection. We recorded beetles at 30 active and 27 non-active sites during 43.8% of surveys. Our top-ranking model indicated that beetle occupancy probability was positively influenced by the presence of marmot burrows (both active and inactive) and that detection probability was a function of temperature and was highest at +26.5°C. Our model represents the first quantitative, empirically-based occupancy model of Blaps rugosa, and reveals the impact of marmot engineering on the distribution of beetles in a landscape. Our results also suggest that improving the conservation status of marmots will indirectly benefit beetles.

Key words: *Blaps rugosa*, ecosystem engineering, forest steppe, marmot burrow, *Marmota sibirica*, Mongolia

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Introduction

Siberian marmots (*Marmota sibirica* (Radde, 1862) are large (approximately 3.9-4.2 kg as adults) herbivorous rodents that burrow and live colonially. Marmots are highly endangered in Mongolia due to overharvesting for fur and meat (IUCN Red List 'EN'; criteria A2 ad) and have been experiencing significant population declines (62%-75%) across Mongolia (Kolesnikov et al., 2009; Buuveibaatar & Yoshihara, 2012).

Burrowing mammals are keystone ecosystem engineers in many communities because burrowing is an engineering activity that can directly and indirectly alter the availability of resources, has affects at multiple spatial and temporal scales, and has a significant role in community organization (Dickman, 1999; Reichman & Seabloom, 2002).

Siberian marmots are known as ecosystem engineers and their mound building transforms grassland landscapes, creating unique habitats for many other species (Van Staalduinen & Werger, 2007; Davidson et al., 2008; Townsend, 2009). Ecosystem engineers are organisms that control the availability of resources for other species by creating and modifying habitat (Jones et al., 1994). Ecosystem engineers alter habitat in such a way as to reduce physical and biological stresses for other organisms (Crain & Bertness, 2006). We expect that the Siberian marmot has an important role in their ecosystems within their range, and is likely a 'keystone species' (Mills et al., 1993; Adiya, 2000; Townsend & Zahler, 2006), however, little is known about some of its ecological role, and in particular if marmot colonies represent a biodiversity hotspot.

Ecosystem engineering is the physical modification of habitat by a species which creates patches with altered species richness relative to adjacent, unmodified habitats. One marmot family or colony usually has several burrows, including active burrows (summer and wintering burrows) and non-active burrows (Adiya, 2000). Non-active burrows are those which temporarily shelter marmots from carnivores, raptors, and bad weather conditions, when traveling looking for food far from their active burrows. In Eastern Mongolia, where the marmot density is high, one family could have an average of 2.9 (2.1–3.5) non-active burrows, whereas marmots in lower density areas have an average of 4.8 (3.7–5.7) non-active burrows (Kucheruk, 1983).

Marmot colonies also act as primary producers and providers of rich resources of organic materials as well as important shelter in the microenvironment (e.g. microclimate, soil nutrients and moisture) which they create. They are of vital importance for the distribution and structure of soil and ground-dwelling invertebrate communities (Deville, 1927; Zinchenko, 2006). Rodent burrows appear to exert disproportionately large effects on species of Coleoptera, especially Scarabaeidae (Moradi and Ziani 2009, 2010; Ziani and Moradi, 2011) and Leiodidae (Peck and Skelley 2001).

The diversity of Coleoptera found in marmot burrows has been studied by various authors. Zinchenko (1997) recorded 31 species of beetles belonging to three families including Histeridae, Scarabaeidae, and Eucinetidae from burrows of *M. bobak* in Orenburg Province, Russia. Zinchenko (1999, 2002) found 44 species of Scarabaeidae from the burrows of *M. baibacina* in the European part of Russia, and 25 species belonging to five families of beetles from the burrows of *M. bobak* in Kemerovo Province, Russia. In addition, several new species, such as *Atheta mariei, Aleochara marmotae* (Staphylinidae), *Catops joffrei* (Leiodidae), and *Cryptophagus arctomyos* (Cryptophagidae) were found in marmot burrows (Deville, 1927) and Grandinaphodius inferorum (Scarabaeidae) in small rodent burrows (Ziani, 2002). Beetles found in marmot burrows represented the families Scarabaeidae, Histeridae, Phalacridae, Staphylinidae, and Eucinatidae. There was no record of *Blaps rugosa* or other member of the family Tenebrionidae. However, the studies at the same sites did show that species richness and abundance of coprophilous beetles (Scarabaeidae) had negative correlations with domestic herbivore density (Bayartogtokh & Otgonjargal, 2009).

The omnivorous and saprophagous *Blaps rugosa* (Tenebrionidae) is a flightless darkling beetle which is well adapted to semi-arid and arid environments because of specific behavioral and morphological traits. Its body structure and habits allow it to live in the dry and hot habitats. Adults are not attracted to light, and their living activities have clear cycles. The beetles live mostly underground in the burrows of rodents and in natural holes. They also can be found under various objects, such as livestock and wild herbivore dung, logs, accumulated plant debris etc., which serve as shelter. The hatching larvae and beetles hibernate inside rodent burrows and appear above ground at the end of April, when the sun warms the upper soil layers (Sagdi, 1996). The species is known to make use of a defensive gland to protect itself, and it is possible that the gland secretion might be usuable as a crude medicine (Gunbilig & Boland, 2009).

One of the important ecosystem services performed by *B. rugosa* is that the faeces of the darkling beetles, despite their insignificant mass, have a great stimulating effect on cellulose-degrading microflora, which contributes to an increase in the rate of mineralization of plant litter in arid and semi-arid zones (Dorzhieva & Chimitova, 2008, Mordkovich, 2003). In addition, various *Blaps* species become food resources for other animals. For example, *B. femoralis* formed 89.5% of the content of Daurian hedgehog scats (N=38 scats) (Murdoch et al., 2006), and was present in 10.1-12.9% of corsac fox *(Vulpes corsac)* scats (N=996), 9.8-21.6% of red fox *(Vulpes vulpes)* scats (N=1142) (Buyandelger 2008) and ~40% (unpublished data table) of Eurasian badger *(Meles leucurus)* scats (N=116) (50% of Tenebrionidae (Murdoch and Buyandelger 2010). Many birds also feed on the Blaps beetles, including Mongolian Skylark *(Melanocorypha mongolica mongolica)* (Ling, 1992) and Lesser Kestrels *(Falco naumanni)* (Onolragchaa et al., 2017).

In this paper, we estimate *B. rugosa* occurrence in relation to the availability of marmot colonies. More specifically, we examined the influence of colonies on the probability of *B. rugosa* occurring within certain habitat on the landscape. Our general hypothesis was that marmot colonies have a positive influence on *B. rugosa* occupancy probability because burrows offer shelter from environmental conditions and refuges from predation, and also support a high diversity of insects and other prey items. We also examined an alternative hypothesis focused on investigating the influence of forest steppe habitats in Hustai National Park, including open plains, foothills and upper slopes, drainages, and near springs on *B. rugosa* occupancy. Our approach involved 1) developing a set of a priori candidate models that we believed potentially described *B. rugosa* occupancy in the landscape, 2) surveying *B. rugosa* at multiple sites to collect detection and non-detection data, and information on marmot and habitat features associated with each site, and 3) using model selection to rank models to evaluate which best represented the data.

Material and Methods

Study area

We conducted this study in the Hustai National Park, situated 100 km southwest of Ulaanbaatar, the capital city of Mongolia. Hustai National Parkcovers approximately 60,000 has at elevations ranging from 1100 to 1840 m above sea level. The National Park occurs at the southern edge of the forest-steppe zone and includes mountains, plains, dunes, and a river valley. Only 4%, or 2000 ha, of the park is covered by forest and 88% is grassland and shrub-land steppe (Buuveibaatar & Yoshihara 2012). Several dry steppe and mountain steppe vegetation types, which occur in the Mongol Dahuria and Middle Khalkha biogeographical regions, are represented in the park. The region is arid with ≤240 mm of annual precipitation, which falls mostly as rain (80%) between June and August, and air temperature ranges from -40 (average winter temperature -20°C) to +40 (average summer temperature +18°C). The landscape is dominated by mountains of granitic rocks with valleys creating varying habitat types. The vegetation is dominated by bunch grass, *Stipa krylovi*, with *Artemisia adamsii, Artemisia frigida, Agropyron cristatum* and *Cymbaria dahurica* as typical species (van Staalduinen, 2005). Marmot abundance is high there, with population density of 70.6 families/km^2 (Kolesnikov et al., 2009). Grey wolves *(Canis lupus)* and raptors, such as steppe eagle *(Aquila rapax)* and golden eagle *(Aquila chrysaetos)* prey on marmots.

Survey

We surveyed 130 sites (Figure 1), including 45 non-active, 43 active burrow sites and 42 control sites during the summer of 2016. The randomly surveyed sites were selected from an array of elevation outcroppings in variable areas, and from a digitized land cover layer using ArcGIS version 10.3 (ESRI, Redlands California, USA) in combination with information from the rangers of the National Park. We visited all the selected points and identified active and non-active colonies as we observed marmots or saw signs of recent marmot activity, including ≥3 open burrows with fresh scat and tracks at the beginning of the study. The recording of new sites was spaced >500 m apart to ensure independence, and this distance was based on another lizard survey (see Murdoch et al., 2013). We recorded *B. rugosa* occupancy with three repetitions in a plot, and conducted our first survey in June, the second in July, and the third in August.

Each survey site was a 25 m radius circular plot. We estimated air temperature and wind speed (at the plot center) using a handheld weather station (measured with a Kestrel 3000 Pocket Weather Meter) at the beginning of each survey, then an observer walked through the plot in a circlular pattern for 5 min, and recorded whether the beetles were present (1) or absent (0). We based the survey time on trials before the study began that indicated *B. rugosa* were usually quickly detected.

At each site, we quantified habitat on the basis of substrate. Habitats were classified by aspect/elevation 1) foothill, which included a low hill at the base of the mountain, 2) upper slope, which included the side of a hill or mountain, 3) open plain, which included gently rolling gravel plains of short grasses and forbs, or 4) drainage, which included natural removal of surface and sub-surface water from an area.

Survey modeling approach

Occupancy modeling is a statistical tool developed to estimate population parameters and investigate the influence of habitat variables on those parameters (Mackenzie et al., 2002). We used single-season occupancy models implemented in the program PRESENCE (v. 4.4, J. E. Hines, Patuxent Wildlife Research Center, Laurel, Maryland, USA) adjusted for detection probabilities. Models were ranked by their AIC (Akaike Information Criterion) scores corrected for small sample size (AIC_c) and weight (AIC weight) in program PRESENCE for model selection (Burnham & Anderson, 2002). We considered the model with the smallest AICc value to be the best model to fit the data and any model within 2 AICc values as a competing model (Burnham & Anderson 2002). We used Akaike weights to assess the strength of evidence for one model versus another model.

Results

We conducted 390 surveys and detected *B. rugosa* during 43.8% of them. We detected *B. rugosa* at 30 marmot active burrow sites and 27 non-active burrow sites, resulting in a naïve occupancy estimate (i.e., total number of sites where darkling beetles were detected/total number of sites surveyed) of 0.452 across all sites. Air temperature in the survey ranged from +17.4 to +38.0°C (mean ± SD = 24.23±0.26). The mean percent of habitat surrounding sites was: 28±0.2 for foothill, 33±0.1 for drainage, 25±0.2 for open plain and 14±0.1 for upper slope.

Bootstrap analysis indicated that our data fit the assumptions of single-season occupancy modelling (MacKenzie et al., 2002). The χ^2 of the observed data was 11.696 and probability of this value was 0.0594 (mean χ^2 of the bootstraps simulations =5.1267). Given little evidence of lack of fit, we continued with model selection procedures to estimate the weight of evidence of all models in the model set.

Model selection results indicated that *B. rugosa* occupancy is influenced by burrow presence: Marmot burrow ψ(Burrow), p(temp+temp^2) was the best approximating model (Table 1). This model accounted for 55.7% of the AICc weight among the competing models, with no competing model <1.70ΔAIC_c. The exclusion of habitat to the top model produced the 2nd ranked model (AICc weight = 23.8), and followed by exclusion detection probability from the top model (Table 1, AIC_c weight = 14.5%). The model which included burrow as a variable was >70.24%, and habitat+burrow was <29.75%.

The remaining models were ≥19.2 ΔAICc from the best model. Beta (β) coefficients for both the active burrow sites and non-active burrow sites were positive, indicating that with a higher percent of these marmot colonies around a given site on the landscape, occupancy probability increased (Table 2). Confidence intervals (95%) around these betas also did not cross zero, suggesting that the effect of these parameters on occupancy was real (Table 2). Additionally, aspect/elevation had little influence on the *B. rugosa* occupancy.

Our top model estimated the effect of temperature on detection probability. Beta estimates from the model (Table 2) indicated that detection probability was >37% between +20.8°C and +27.1°C (Figure 2). B. rugosa detection probability was highest at approximately +26.5°C.

Discussion

This study is consistent with the hypothesis that Siberian marmot may be keystone species for certain species' occupancy due to their engineering activities (Murdoch et al., 2013). Our results show that ecosystem engineering by Siberian marmot had keystone-level effects on *B. rugosa* occupancy in all types of habitat in the study area. *B. rugosa* occupancy 55.7% in relation to marmot burrows ± detection probability.. Especially interesting was our finding that habitat diversity and elevation did not affect the beetles' occupancy. The occupancy of many other invertebrates is largely associated with rodent burrows. The reason may be the availability of habitat patches, through ecosystem engineering (Bangert & Slobodchikoff, 2006; Davidson & Lightfoot, 2007; Kenney et al., 2016), food resources (Zinchenko, 1997, 1999, 2002; Peck & Skelley, 2001; Moradi & Ziani, 2009, 2010; Ziani & Moradi, 2011), shelter (Adiya, 2000; Nikol'skii, 2003), and increased nitrogen level in soils for oviposition(Dempster, 1963).

Burrowing reduces soil bulk density, which in turn increases water infiltration into the soil, as well as the concentration of soil nutrients, such as carbon, nitrogen and phosphorus (Gabet et al., 2003; Eldridge et al., 2012). Burrowing activity by marmots indirectly creates favorable microhabitat for plant communities by a physical process that mixes and aerates soil layers (Townsend, 2006; Yoshihara et al., 2010b). By providing key habitat with high concentration of resources, rodent burrows enhance population, species richness, and occupancy for various taxonomic groups. The insect-pollinated plant productivity promoted by marmot ecosystem engineering supports pollinators (Yoshihara et al., 2010a). Furthermore, we very often observed the darkling beetles at the entrance of marmot burrows. Burrow entrances are usually surrounded by bare soil and short-turf vegetation. Cizek et al. (2012) showed that *B. lethifera* was associated with bare-ground patches, especially rodent burrows.

The strong association of omnivorous *B. rugosa* with marmot burrows appears to be in large part because burrows provided food sources. Other studies showed that keratinophilic fungi, especially *Microsporum gypseum* had greater occurrence in marmot burrow soil than in the surrounding area (Battelli, 1978). *B. rugosa* can use marmot faeces as their food resource, in the same manner as dung beetles. Also, *B. rugosa* probably feeds as a scavenger on decomposing nest matter or microorganisms growing on the marmot faeces in the burrow, same as carrion beetles (Peck & Skelley, 2001).

Darkling beetle occupancy is not only limited to the active burrow sites. They also occur in non-active marmot burrows (see Figure 3). The non-active burrow, which is usually farther away from the active burrow, is also used by species besides marmots (Kucheruk, 1983). *B. rugosa* may not use burrows only as a food source , but also for shelter from extreme environmental conditions. Microclimate in marmot burrows is relatively stable, not overheating even in hot weather, and remains above freezing even with significant decreases in air temperature on the soil surface (Adiya, 2000; Nikol'skii, 2003). The high moisture content is probably advantageous to many species, especially in arid environments where evaporative water loss may be significant above ground, although high relative humidity may restrict evaporative cooling in animals, which may be a problem for individuals with excessively high body temperatures (Reichman & Smith, 1990). Rodent burrows also support species richness as many beetles, including those from the families Leiodidae, Staphylinidae, Carabidae, Scarabaeidae etc. use marmot droppings as a food resource for themselves and their larvae.

Another alternative hypothesis for the co-occurrence of rodents and beetles is that beetles lay their eggs in rodent burrows. Species searching for a substrate upon which to oviposit must be guided in the darkness by an acute sense of smell (Pont & Ackland, 1995). Therefore, for the darkling beetle the oviposition process might include the need for conditions such as the presence of animal droppings, burrows, or caves etc. McIntyre (1999) showed that some darkling beetles use ant nest-sites for oviposition and thermoregulation in the grasslands of North America. However, at our research site, darkling beetle occupancy was significantly influenced by marmot burrow presence not only in the breeding season of the beetle but also during non-breeding periods.

The ecosystem engineering concept focuses on how organisms physically change their landscape and how these changes create feedback mechanisms that affect the biota of these sites (Jones et al., 1994). Our research results give insight into how marmots create important habitats for the darkling beetle and demonstrate that engineering species have an irreplaceable role in this ecosystem. Marmot burrows provide a network of basking sites for thermoregulation, foraging locations, and refuge for *B. rugosa* across the landscape, likely resulting in more favorable habitat and higher survivorship at the landscape-scale. Our occupancy analysis supports our hypothesis that marmot colonies have a positive influence on *B. rugosa* occupancy probability because burrows offer shelter from extreme environmental conditions, refuges from predation, and support a high diversity of insects and other prey items.

Our model is the first quantitative, empirically based occupancy model of *B. rugosa*, and may be adaptable for analysis of different ecosystems with marmots in Mongolia. Further studies should consider examining the *B. rugosa* diet, the relationship between marmot burrows and *B. rugosa* food preferences, the ontogenetic life history of this darkling beetle species, and importance burrows for the species' larval development. Other burrow digging rodents may influence darkling beetle occupancy in the steppe ecosystem. We focused on marmot colonies and habitat types at one spatial scale. It is possible that *B. rugosa* occupancy may also be influenced by other predators (e.g. hedgehog, badger and birds) and sympatric species (e.g., *B. reflexa and Carabus spp.*), and further studies should consider assessing patterns of co-occurrence with these species.

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***Table 1.** Response variables used to examine Blaps rugosa occupancy probability (ψ) in Hustai National Park, from June to August 2016.*

Covariate name	Description	Measure	Predicted effect on ψ	Supporting Literature
Burrow	Occupancy probability influenced by active burrow site and in non-active burrow.	Active and non-active	Positive	Murdoch et al, 2009, 2013, 2016; Shipley and Reading 2006
Upper slope	Including the side of a hill or mountain	Proportion	Negative	Todgerel 1998, Yoshihara et al, 2010 b
Foothill	Including a low hill at the base of a mountain	Proportion	Positive	Todgerel 1998, Yoshihara et al, 2010b
Drainage	Including natural removal of surface and sub-surface water from an area	Proportion	Positive	Todgerel 1998, Yoshihara et al, 2010b
Open plain	Including gently rolling gravel plains of short grasses and forbs	Proportion	Positive	Murdoch et al, 2013, 2016, Yoshihara et al, 2010 b

***Table 2.** Model selection results of Blaps rugosa probability of occupancy (ψ) indicating the fit of 8 models to the observed data collected in Hustai National Park, from June to August 2016. Occupancy covariates included: presence on marmot burrow site, and habitat including foothill, open plain, drainage and upper slope within 250 m of a site.*

Model	AIC	deltaAIC	AIC wgt	Model Likelihood	no.Par.
psi(Burrow),p(temp+temp^2)	371	0	0.5572	1	5
psi(Burrow+Habitat),p(temp+temp_sq)	373.65	1.70	0.2382	02328	6
psi(Burrow),p(.)	374.64	2.69	0.1452	0.1065	3
psi(Burrow+Habitat),p(.)	376.43	4.48	0.0593	0.1065	4
psi(.),p(temp+temp2)	391.21	19.26	0.0000	0.0001	4
psi(Habitat),p(temp+temp2)	392.76	20.81	0.0000	0.0000	5
psi(.),p(.)	394.16	22.21	0.0000	0.0000	2
psi(Habitat),p(.)	395.77	23.82	0.0000	0.0000	3

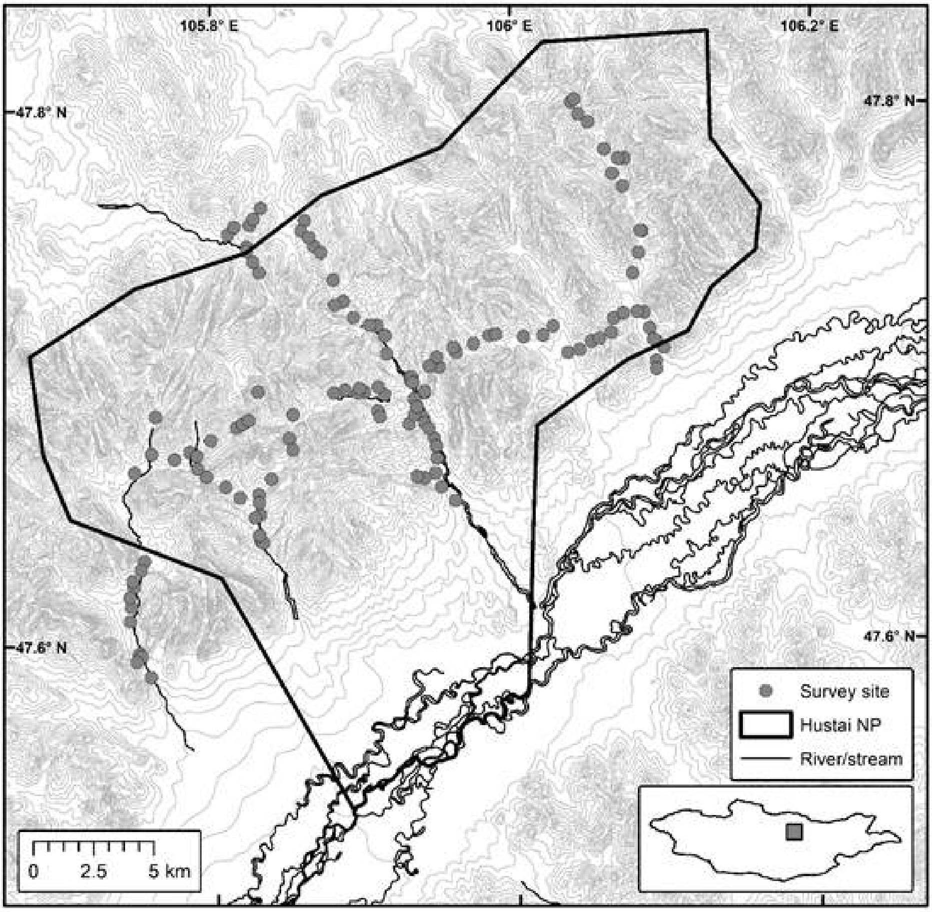

Figure 1. *Map of the study area in Hustai National Park, Mongolia, showing the survey spots in the main areas of marmot distribution.*

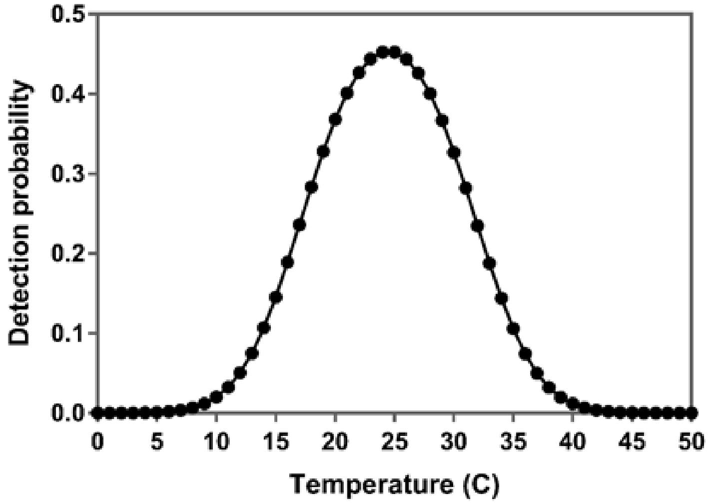

Figure 2. *Blaps rugosa probability of detection p(temp+temp2) as a function of temperature. Probability estimated from the top-ranking model of occupancy data collected in Hustai National Park, from June to August 2016.*

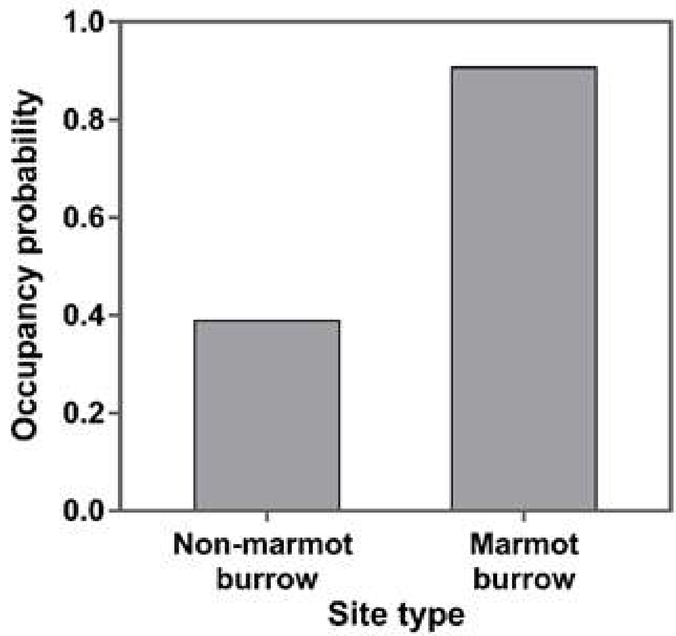

Figure 3. *Blaps rugosa occupancy probability ψ(Burrow) as a function of the proportion of marmot burrow site within 250 m of each location. Probability estimated from the top-ranking model of occupancy data collected in Hustai National Park, from June to August 2016.*