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Do Siberian marmots influence toad-headed agama occupancy? Examining the influence of marmot colonies and three steppe habitats in Mongolia

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ABSTRACT

The Siberian marmot is a large, endangered rodent and often considered a keystone species because of its perceived effects on steppe ecosystems. However, few studies have examined the effects of marmots on other species. We examined the influence of marmots on toad-headed agama occupancy probability in an arid steppe region of Mongolia. We modeled the influence of marmot colonies and three habitats, including rocky outcrops, open plains, and shrubland using an occupancy modeling framework based on three surveys of 122 sites from June to August 2010. We detected agamas during 64% of surveys and at 85% of sites. Marmot colonies and their interactions with other habitats had little influence on occupancy probability at a given site. The amount of surrounding open plains and shrubland also showed little influence. Our results indicated toad-headed agama occupancy was inversely related to the amount of surrounding rocky outcrop. Rocky outcrop may be less suitable to agamas because of its sparse vegetation, lack of burrows, and heat-absorbing qualities. Although marmots affect the distribution of other species, our results suggest they exert little influence on toad-headed agamas. We also suggest that the creation of rocky habitat by mineral mining will negatively impact toad-headed agamas.

1. Introduction

Keystone species exert a disproportionately large effect on an ecosystem than expected by their abundance, and can influence the distribution of other species (Kotliar, 2000; Power et al., 1996). The Siberian marmot (*Marmota sibirica*) is often considered a keystone species in northern Asia (Zahler et al., 2004). The species is a large (c. 6–8 kg), social rodent that occurs throughout Mongolia and adjacent regions in Russia (Siberia) and China (Batbold et al., 2008). Marmots live in colonies that can cover several hectares and include multiple (sometimes >90) subterranean burrow entrances (Townsend, 2006). The species is thought to be a keystone because it affects plant communities by digging burrows that aerate soils and recycle nutrients, and serves as an important prey species for several raptors and carnivores (Ellis et al., 1999; Heptner and Naumov, 1992; Murdoch et al., 2009; Van Staalduinen and Werger, 2007; Zahler et al., 2004). Its burrows also provide shelter and refuges for insects, lizards, and mammals, and may be preferred habitat for some species (Adiya, 2000). Although marmot colonies influence the distribution of some species, such as corsac foxes (*Vulpes corsac*) and Pallas's cats (*Otocolobus manul*) that actively use their burrows (Murdoch et al., 2009; Ross et al., 2010), few studies have examined their role on other smaller species (Zahler et al., 2004). Understanding the influence of marmots is a conservation priority in range countries because the species is endangered and rapidly declining throughout most of its range (Batbold et al., 2008; Clark et al., 2006).

We examined the influence of marmots on the toad-headed agama (*Phrynocephalus versicolor*). Toad-headed agama is a small, arid-adapted Agamidae lizard that occurs throughout Mongolia and northern Asia (Ananjeva et al., 1997; Terbish et al., 2006). The species is common and probably represents the most abundant vertebrate in some regions as it can reach densities >100 individuals/ha (Murdoch et al., 2010; Rogovin et al., 2001). Toad-headed agamas are rarely the focus of management and conservation efforts because of their high abundance, but other studies suggested that they represent an important prey item for some threatened species (e.g., saker falcon, *Falco cherrug*, Gombobaatar et al., 2001; lesser kestrel, *Falco naummani*, Suuri et al., 2012). Their high abundance also probably influences community structure and function (Rogovin et al., 2001).

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The objective of our study was to examine whether marmot colonies influence the distribution of toad-headed agamas. More specifically, we examined the influence of colonies on the probability of an agama occurring at a given site in the landscape. Our general hypothesis was that colonies have a positive influence on agama 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 alternative hypotheses focused on the influence of common steppe habitats of northern Asia, including rocky outcrops, open plains, and shrubland. Our approach involved 1) developing a set of *a priori* candidate models that we believed potentially described agama occupancy in the landscape, 2) surveying agamas 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.

2. Methods

2.1. Study area

We conducted the study in Ikh Nart Nature Reserve, located in Dornogobi Aimag, Mongolia (45°43′N–108°39′E). Ikh Nart is a 666 km^2 reserve established in 1996 to protect a population of argali sheep (*Ovis ammon*) and the unique landscape of the region (Myagmarsuren, 2000). The reserve occurs at the margin of steppe and semi-desert ecozones and includes a variety of steppe flora and fauna (Reading et al., 2011). The region is arid with <200 mm of annual precipitation, which falls mostly as rain from June to August (summer), and temperature ranges from −40 to +43 °C. Toad-headed agamas occur throughout the reserve and in high density relative to other lizards (Murdoch et al., 2010). Other sympatric and less common species include Mongolian racerunner (*Eremias argus*), multi-cellated racerunner (*Eremias multiocellata*), and Przewalski's racerunner (*Eremias przewalskii*) (Reading et al., 2011; Terbish et al., 2006). Toad-headed agamas hibernate during winter and are generally active from April to October.

2.2. Surveys

We surveyed 122 sites, including 60 random sites and 62 marmot colony sites, in summer of 2010. Marmot colonies were identified by a systematic survey of the study area in 2009 (S. Buyandelger, unpublished data). The survey identified 115 colonies and we selected those that were active at the beginning of the study ($n = 62$). We defined an active marmot colony as one that exhibited signs of recent marmot activity, including ≥3 open burrows with fresh scat and tracks. Sites were spaced >500 m to ensure independence. We based this distance on previous observations of agamas in the study area that suggested individuals occupied small ranges that would not overlap at this scale. Marmot colony sites were established at the geometric center of a minimum convex polygon enclosing all burrows of a colony. We surveyed each site three times. The first survey occurred in June, the second in July, and the third in August.

Each survey site was a 25-m radius circular plot. For each survey, we marked the plot, then waited for 15-min at a distance of >100 m before beginning the survey to minimize the influence of the surveyor. We estimated surface temperature (at the plot center) using a handheld thermometer (Instant Read Pocket Thermometer, Taylor, Oak Brook, Illinois, USA) at the beginning of each survey, then an observer walked through the plot in a zig-zag pattern for 5-min and recorded whether agamas were present (1) or absent (0). We based the survey time on trials before the study began that indicated agamas were usually quickly detected and longer survey periods did not yield new detections. All surveys occurred between 1000 and 1400 h.

At each site, we quantified habitats on the basis of substrate and vegetation characteristics. Habitats were 1) rocky outcrops, which included rugged, rocky substrate (igneous and metamorphic) with sparse vegetation, 2) open plains, which included gently rolling, sand and gravel plains of short grasses and forbs, and 3) shrubland, which included sandy areas dominated by shrubs and tall grasses (>0.5 m). We selected these habitats because we believed they meaningfully affected lizard distribution and to be consistent with previous surveys of the species (Murdoch et al., 2010). These habitats occurred in relatively equal amounts in the study area (Jackson et al., 2006). We estimated the proportion of each habitat type within 25-m, 250-m, and 500-m radii of each plot using Geographic Information Systems (ArcGIS v. 9, ESRI, Redlands, California, USA) and habitat maps derived from a classification of Landsat imagery (Jackson et al., 2006). Spearman's rank correlation indicated significant correlations ($p < 0.05$) between habitats at these scales, so we only used 250-m values in the analysis.

2.3. Modeling approach

We used an occupancy modeling framework to examine the influence of marmot colonies and habitats on the occurrence of agamas. Our aim was to estimate the influence of marmot colonies and habitats on the probability of occupancy at a given site in the landscape. Occupancy modeling uses the multinomial maximum likelihood function to estimate a species' occupancy probability (ψ) given a set of detection and non-detection survey data (MacKenzie et al., 2002). An advantage of this approach is that it accounts for the imperfect detection of a species (*i.e.*, the probability of a species occurring in an area, even when it goes undetected during surveys) by incorporating detection probability (p) when estimating occupancy probability (MacKenzie et al., 2002).

2.4. Model set

We developed 16 candidate models, with each model estimating both the factors that affect probability of occupancy (ψ) and probability of detection (p) (Table 1). For instance, model $\psi(m).p(temp + temp^2)$ represented a model where occupancy at a site was a function of the presence or absence of a marmot colony, and detection at a site was a function of the temperature during which a survey was conducted.

In terms of detection probability, all 16 models included temperature as a detection covariate because agamas are ectothermic and activity is influenced by temperature. Previous studies indicated that agamas were most active between 25 and 35 °C and retreated to burrows when temperature fell outside of this range (Murdoch et al., 2010), thus affecting the probability that an observer would detect an agama if present. However, the optimal temperature conditions for toad-headed agamas have not been quantified. We modeled temperature as a polynomial (temperature + $temperature^2$) because the relationship between temperature and activity is not linear.

In terms of occupancy probability, models included the influence of marmot colony, each individual habitat, additive combinations of the three habitats, and the interaction of marmot colony and each habitat. For example, model $\psi(sh)$ represented a model where occupancy is a function of the percent shrubland (sh) within 250 m of the site, while model $\psi(ro + op + sh + m)$ represented a model where occupancy was a function of the percent rocky outcrop (ro), open plains (op), and shrubland within 250 m of a site, in addition to whether the site was within a marmot colony (m) (Table 1). The most complex models included interactions between

Table 1
Model selection results of toad-headed agama (*Phrynocephalus versicolor*) probability of occupancy (ψ) indicating the fit of 16 models to the observed data collected in Ikh Nart Nature Reserve, Mongolia from June to August, 2010. All models included temperature (modeled as a polynomial: $temp + temp^2$) as a detection (p) covariate. Occupancy covariates included: presence on marmot colony (m) and amount of rocky outcrops (ro), open plains (op), and shrubland (sh) within 250 m of a site. We considered the top ranking model: $\psi(ro)$, $p(temp + temp^2)$ to be the best model in the set.

Model	AIC	ΔAIC	AIC weight	Model likelihood	No. of parameters	−2*LogLike
$\psi(ro)$, $p(temp + temp^2)$	422.06	0	0.3678	1	5	412.06
$\psi(ro + op)$, $p(temp + temp^2)$	424.06	2.00	0.1353	0.3679	6	412.06
$\psi(ro + sh)$, $p(temp + temp^2)$	424.06	2.00	0.1353	0.3679	6	412.06
$\psi(ro + m + m^*ro)$, $p(temp + temp^2)$	424.63	2.57	0.1018	0.2767	7	410.63
$\psi(ro + op + sh)$, $p(temp + temp^2)$	425.47	3.41	0.0669	0.1818	7	411.47
$\psi(ro + sh + m)$, $p(temp + temp^2)$	425.66	3.60	0.0608	0.1653	7	411.66
$\psi(ro + op + m)$, $p(temp + temp^2)$	425.68	3.62	0.0602	0.1637	7	411.68
$\psi(ro + op + sh + m)$, $p(temp + temp^2)$	426.98	4.92	0.0314	0.0854	8	410.98
$\psi(op + sh)$, $p(temp + temp^2)$	427.20	5.14	0.0281	0.0765	6	415.20
$\psi(op + sh + m)$, $p(temp + temp^2)$	428.87	6.81	0.0122	0.0332	7	414.87
$\psi(sh + m + m^*sh)$, $p(temp + temp^2)$	438.03	15.97	0.0001	0.0003	7	424.03
$\psi(m)$, $p(temp + temp^2)$	440.92	18.86	0	0.0001	5	430.92
$\psi(sh)$, $p(temp + temp^2)$	441.17	19.11	0	0.0001	5	431.17
$\psi(op + m + m^*op)$, $p(temp + temp^2)$	442.92	20.86	0	0	7	428.92
$\psi(op)$, $p(temp + temp^2)$	443.31	21.25	0	0	5	433.31
$\psi(.)$, $p(temp + temp^2)$	443.43	21.37	0	0	4	435.43

marmots and a habitat feature, such as model $\psi(ro + m + m^*ro)$, which let the effect of rocky outcrops on occupancy probability vary depending on whether the site was a marmot colony site or not.

The four occupancy covariates (marmot colony, rocky outcrops, open plains, and shrubland) were equally represented in the model set (Table 1). That is, the effect of each covariate was estimated in 8 of the 16 models. This enabled us to use "variable importance" analysis to assess which of the four covariates most affected occupancy probability (Burnham and Anderson, 2010).

2.5. Occupancy and model selection

We calculated detection histories for each site (e.g., a history of '101', indicated that we detected the species in survey 1 and 3, but not in survey 2) and applied a single-season, single species occupancy model to estimate detection and occupancy probability (MacKenzie et al., 2002). We fit our 16 models using Program Presence (v. 4.4, J. E. Hines, Patuxent Wildlife Research Center, Laurel, Maryland, USA). Models were ranked by their AIC (Akaike Information Criterion) scores and weighted (AIC weight) as the probability of being the best model in the model set (Burnham and Anderson, 2010). We used a goodness-of-fit test on the most parameterized model to examine how well it fit the observed data. This is necessary in multi-model inference to demonstrate that at least one model in the model set fits the observed data (otherwise the AIC ranks are meaningless). We estimated the fit of the most parameterized model: $\psi(ro + op + sh + m)$, $p(temp + temp^2)$ using a parametric bootstrap procedure with 100 simulations (MacKenzie and Bailey, 2004). The importance of each variable (covariate) was estimated as the sum of the AIC weights for models in which the covariate was estimated (Burnham and Anderson, 2010).

3. Results

3.1. Surveys

We conducted 366 surveys and detected agamas during 64% of them. We detected agamas at 47 random sites and 57 marmot colony sites, resulting in a naïve occupancy estimate (*i.e.*, total number of sites where agamas detected/total number of sites surveyed) of 85% across all sites. Temperature at each survey varied from 10.9 to 37.7 °C (mean ± SE = 23.1 ± 0.25 °C). The mean percent of habitat surrounding sites was: 10 ± 0.1 SE for rocky outcrops, 40 ± 0.1 SE for open plains, and 50 ± 0.2 SE for shrubland.

3.2. Goodness-of-fit

Bootstrap analysis indicated that our data fit the assumptions of single-season occupancy modeling (MacKenzie et al., 2002). The χ^2 of the observed data was 9.4183 and probability of this value was 0.2376 (mean χ^2 of the bootstrap simulations = 8.4296). Given little evidence of lack of fit, we used model selection procedures to estimate the weight of evidence of all models in the model set.

3.3. Model selection

The top ranking model included only rocky habitat as an occupancy covariate ($\psi(ro)$, $p(temp + temp^2)$; Table 1). This model had strong support relative to other models in the set based on its AIC weight of 0.3678. Beta (β) estimates for this model (Table 2) indicated that occupancy was inversely proportional to the amount of surrounding rocky habitat (Fig. 1). However, two other models had

Table 2
Parameter estimates with standard errors (SE) and upper (UCI) and lower (LCI) confidence intervals for the top three ranked models of toad-headed agama (*Phrynocephalus versicolor*) occupancy data collected in Ikh Nart Nature Reserve, Mongolia from June to August, 2010. Occupancy (ψ) parameters included an intercept and habitat (rocky outcrop, open plain, shrubland). Detection (p) parameters included an intercept and temperature (modeled as a polynomial: temperature + temperature^2). We considered Model 1 to be the best model among the three.

Parameter	β estimate	SE	UCI	LCI
Model 1 − $\psi(ro)$, $p(temp + temp^2)$				
ψ intercept	2.927	0.458	3.823	2.030
Rocky outcrop	−7.679	1.857	−4.038	−11.320
p intercept	−6.060	1.608	−2.909	−9.211
Temperature	5.585	1.401	8.330	2.839
Temperature^2	−1.034	0.301	−0.445	−1.623
Model 2 − $\psi(ro + op)$, $p(temp + temp^2)$				
ψ intercept	2.971	0.853	4.643	1.299
Rocky outcrop	−7.715	1.945	−3.903	−11.527
Open plain	−0.101	1.610	3.055	−3.257
p intercept	−6.065	1.599	−2.931	−9.199
Temperature	5.589	1.392	8.317	2.861
Temperature^2	−1.035	0.299	−0.449	−1.621
Model 3 − $\psi(ro + sh)$, $p(temp + temp^2)$				
ψ intercept	2.972	0.992	4.916	1.028
Rocky outcrop	−7.730	2.111	−3.592	−11.868
Shrubland	−0.083	1.604	3.061	−3.227
p intercept	−6.056	1.617	−2.887	−9.225
Temperature	5.581	1.409	8.343	2.819
Temperature^2	−1.033	0.302	−0.441	−1.625

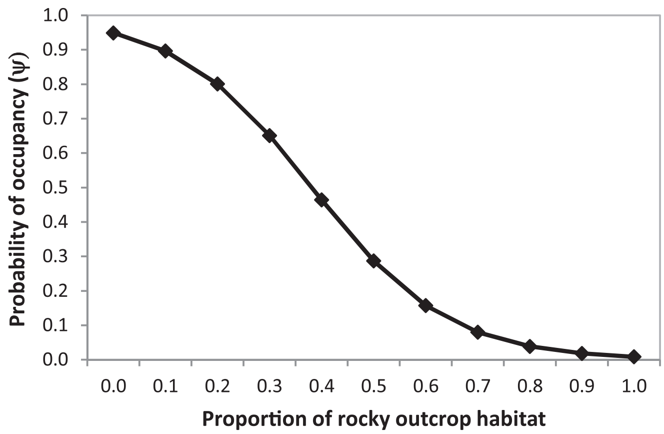

Fig. 1. Toad-headed agama (*Phrynocephalus versicolor*) probability of occupancy (ψ) as a function of the proportion of rocky outcrop habitat within 250 m of a site. Probability estimated from the top ranking model of occupancy data collected in Ikh Nart Nature Reserve, Mongolia from June to August, 2010.

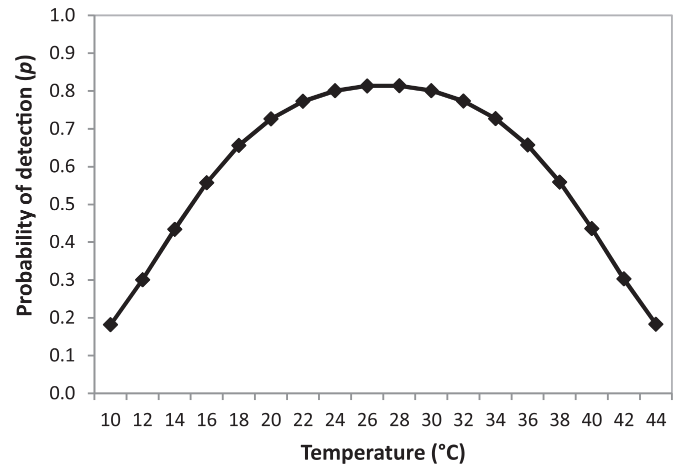

Fig. 2. Toad-headed agama (*Phrynocephalus versicolor*) probability of detection (p) as a function of temperature. Probability estimated from the top ranking model of occupancy data collected in Ikh Nart Nature Reserve, Mongolia from June to August, 2010.

the same -2*Log Likelihood estimate, model $\psi(ro + op)$, $p(temp + temp^2)$ and model $(ro + sh)$, $p(temp + temp^2)$, indicating that the fit for these models was identical to the top model and that the ΔAIC scores and lower AIC weights (0.1353 for both) simply reflected the fact that these models estimated one additional parameter (Table 1). In both of these models, the beta values for rocky outcrops were similar. For the additional habitat parameters (open plain and shrubland, respectively), beta values were near zero. Confidence intervals around these betas also included zero indicating that the effect of these parameters was probably negligible.

Variable importance analysis revealed that rocky outcrop was the most important factor influencing lizard occupancy (0.9595; Table 1). By comparison, variable importance for open plains was 0.3341 and shrubland was 0.3348. The importance of marmot colony was lowest at 0.2665 (Table 1). Furthermore, models including marmot colony as a covariate had little support (Table 1). With the exception of models including rocky outcrop and marmot colony together, all other marmot colony models (including interactions with other habitats) had ΔAIC scores of >6.8, indicating little empirical support (Burnham and Anderson, 2010). The lowest ranking model in our set included no covariates and hence the fewest parameters (Table 1).

Our top model estimated the effect of temperature on detection probability. Beta estimates from the model (Table 2) indicated that detection probability was >75% between 22 and 32 °C (Fig. 2). Agama detection was highest at approximately 27 °C (Fig. 2).

4. Discussion

Our results suggest that marmots exert little influence on the distribution of toad-headed agamas. Although marmots are often considered a keystone species, their colonies did not meaningfully affect the occupancy probability of the species at a given site in the landscape. Marmots appear to exert disproportionately large effects on other species, but their effects on toad-headed agamas, and probably other desert Agamidae, appear negligible.

Our results suggest that marmot burrows and conditions on colonies do not affect habitat quality for the species. However, our study only assessed the influence of active marmot colonies, or those occupied by the species, and inactive colonies, or those that have been abandoned or where all marmots have been harvested, may affect agama occupancy over time. Marmots often influence soils and plant species composition and structure, and these changes may affect habitat quality (and ultimately conditions for occupancy) for agamas. Marmot abundance in colonies may also exert an effect, but we were unable to account for this in our analyses. Similarly, marmots may influence the local abundance of agamas, which occurred at a majority of marmot colony sites. Our study focused on occupancy rather than abundance, but future studies should consider examining the relationship between marmot and agama abundance.

Type of habitat appeared to influence patterns of toad-headed agama occupancy. Of three common steppe habitats, rocky outcrop appeared to exert the most influence on toad-headed agama occupancy. Rocky outcrops were characterized by rugged, rocky terrain, with sparse vegetation, and the amount of this habitat at a given site inversely influenced occupancy probability. This inverse relationship was probably due to the lack of vegetation, which may make agamas more vulnerable to predation, and lack of suitable substrate for burrows. It may also be due to the heat-absorbing qualities of rocky substrate, which increases in temperature more rapidly than substrates typical of other steppe habitats. This may affect the ability of agamas to effectively thermo-regulate and potentially the distribution of prey and other food items.

The influence of rocky areas on agama distribution has conservation implications. In Ikh Nart Nature Reserve, illegal mining for amethyst quartz occurs commonly (Reading et al., 2011). Miners typically establish a temporary camp, then dig large pits to extract the mineral. Extraction results in extensive tailing piles that are left after a seam has been mined. The process essentially creates rocky habitat, which may result in localized changes in agama distribution. Illegal mining is a priority conservation issue for the reserve, and increasing elsewhere in Mongolia, including protected areas (Farrington, 2005).

Our results also provide a measure of the effect of temperature on agama detection. Agamas may be active at a variety of temperatures (Murdoch et al., 2010). However, the probability of detecting the species at a given site was greatest at 27 °C based on our model. Furthermore, our model estimated that detection probability is >75% between 22 and 32 °C. We recommend this range for researchers undertaking studies that aim to maximize detection of the species. However, it is important to recognize that we modeled the relationship between agama detection and temperature as a polynomial and it is possible that another type of relationship may exist.

A limitation of our study is that it occurred in a small portion of toad-headed agama range. It is possible that patterns of agama occupancy elsewhere may be different. However, we focused on broad habitat types that generally occur throughout the species range, and believe that patterns we observed are probably similar in other steppe regions of Mongolia. Additional study areas would be helpful for providing a comprehensive picture of agama occupancy and distribution. However, additional study areas across agama range may be costly and impractical, so other methods, such as incorporating expert opinion, should be considered (Murray et al., 2009). Expert opinion may also provide finer-scale habitat preferences at our site that could strengthen our assessment of agama occupancy in the Ikh Nart region.

Other factors may influence agama occupancy in steppe ecosystems. We focused on marmot colonies and habitat types at one spatial scale. However, analyses at multiple-spatial scales often reveal more details on the relationships between a species and its environment, especially with respect to occupancy (Murray et al., 2008). Fine-scale habitat factors, such as soil type (important for burrowing) or vegetation composition and structure at survey sites may improve our assessment of occupancy. It is possible that agama occupancy may also be influenced by other sympatric species (e.g., *E. argus*, *E. multiocellata*) through competition, and future studies should consider assessing patterns of species co-occurrence (MacKenzie et al., 2004).

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