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Habitat requirements of the long-tailed ground squirrel (*Spermophilus undulatus*) in the southern Altai

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Abstract

The long-tailed ground squirrels *Spermophilus undulatus* represent the most abundant burrowing herbivorous species in the southern Altai grasslands and are suggested to play an important role in the maintenance of this mountain ecosystem. The aim of this study was to identify the key features that influence their habitat use in the southern part of the Altai Republic (south-west Siberia, Russia). The research area represents a complete sequence of altitudinal vegetation zones from steppe, forest-steppe, forest, sub-alpine and alpine tundra. Our results suggest that *S. undulatus* prefers short-grass steppes, near the water source and with a thin layer of a chernozem soil containing a large amount of coarse clastics. The species strictly avoids forests and tolerates only a low density of bush cover. Altitude and exposure to sun do not represent significant factors in the habitat choice of *S. undulatus*. Neither the presence of pikas nor the presence of marmots influences habitat selection of the ground squirrels. Strong preferences for habitats near a water source may limit the distribution of the species to mountain areas. Degree of human disturbance was not a significant factor affecting distribution and the species even displays slight preferences for heavily grazed habitat near human settlements and roads. Intensive grazing prevents shrubs and forest invasion, keeps vegetation low and thus provides appropriate conditions for the ground squirrels, favouring an open habitat where predators can be easily detected by sight. Our results suggest that the habitat selection of ground squirrels may be determined rather by a protection from predators and burrowing conditions than by food availability.

Introduction

The Altai Mountains have global conservation importance, as they encompass biological features from Siberian taiga to Central Asian mountain, steppe and semi-desert ecosystems. The Altai Mountains are considered a centre of plant diversity for montane conifer and alpine meadow ecosystems in Central Asia (Kuchin, 2001).

Long-tailed ground squirrels *Spermophilus undulatus* (Pallas, 1778), hereafter ground squirrels, represent the most abundant burrowing species in the southern Altai montane steppe. In Altai mountain plateaux, colonies may occupy even 50% of the mountain steppe habitat (Tupikova, 1989). The highest density has been observed in the river valley steppe habitat, where the number of burrows reaches up to 96 per 1 ha (Kuchin, 2001). In southern Tuva, ground squirrels occupy intermountain valleys dominated by grasses and sagebrush vegetation (Shilova *et al*., 1979).

Ground squirrels are suggested to play an important role in the maintenance of the Altai Mountain ecosystem. They represent an important prey species for many predators in the Altai Mountains, for example Pallas's cats *Otocolobus manul*, snow leopards *Uncia uncia*, wolves *Canis lupus*, corsac foxes *Vulpes corsac*, mountain weasels *Mustela altaica* and steppe polecats *Mustela eversmanni* (Flint, Chugunov & Smirin, 1965; Aristov & Baryshnikov, 2001; Kuchin, 2001). They are also included in the diet of birds of prey: saker falcon *Falco cherrug*, imperial eagle *Aquila heliaca*, tawny eagle *Aquila rapax* or golden eagle *Aquila chrysaetos* (Malkov, 1996). Therefore, the risk of predation may strongly influence the decision-making processes of this ground squirrel, as has been shown with other species of ground-dwelling squirrels (e.g. Armitage,

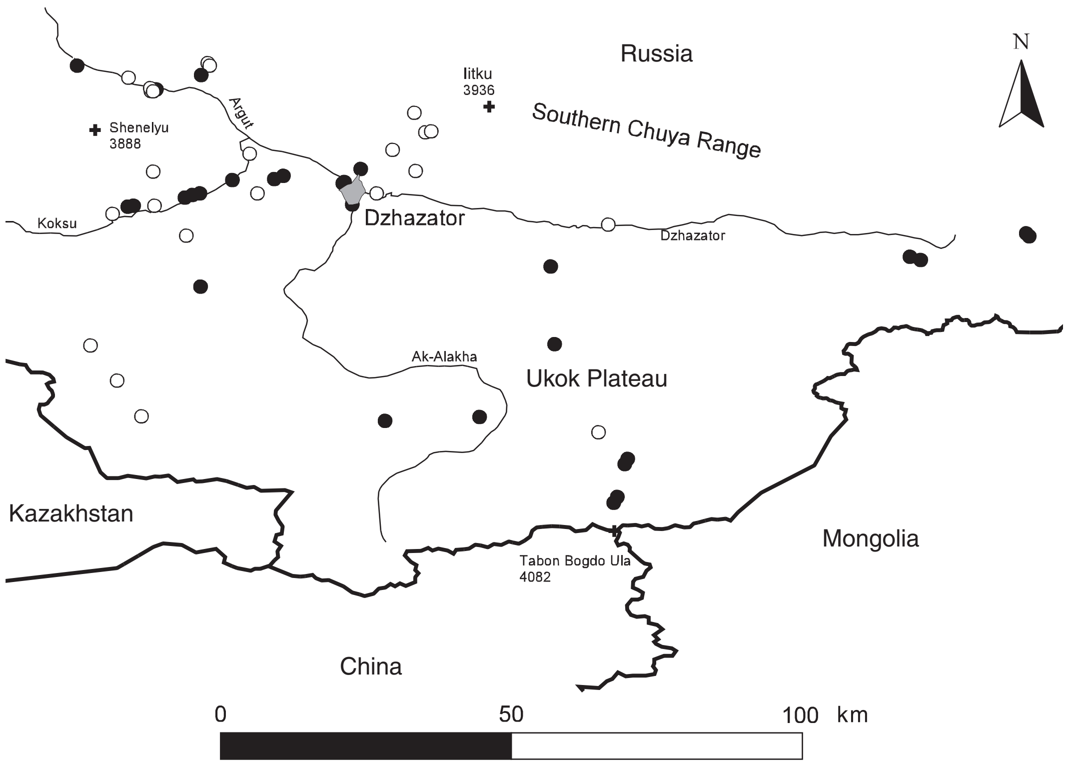

Figure 1 Location map of the study area in the southern Altai Mountains, Altai Republic, Russia. Black circles, transects with ground squirrels *Spermophilus undulatus*; white circles, transects without ground squirrels.

1982; Holmes, 1984; Carey & Moore, 1986; Sharpe & Van Horne, 1998).

The species largely depends on burrows for a shelter and hibernation refuge. Burrows may be 15 m long, 3 m deep and with several entrances (Flint *et al*., 1965). Environmental conditions influencing burrow construction and micro-environment may play an important role in the species' habitat selection.

Ground squirrels are not dietary specialists; they consume all species of steppe and meadow vegetation (seeds and green parts of plantains, sedges, *Potentilla* and Poaceae) as well as insects (*Coleoptera*, *Caelifera*) (Yudin, Galkina & Potapkina, 1979). Therefore, food availability is not suggested to be a limiting factor in habitat use.

Ground squirrels generally occupy a wide range of habitats, mostly steppes and alpine meadows, but in the northern part of their range they are also found in open taiga forests (Gromov & Erbayeva, 1995). Their whole range includes southern and central Siberia, from Tien – Shan Mountains in the south, through Lake Baikal to the Lena River basin in the north and the Amur River basin in the east (Panteleyev, 1998). The western and central parts of ground squirrel distribution consist of many isolated populations restricted to mountain steppe habitats, and remote Pleistocene relict populations are also found in Yakutia and the Amur region (Gromov & Erbayeva, 1995).

The aim of this study was to identify the main features that influence ground squirrels' habitat selection in the southern part of the Altai Mountains.

Methods

Study area

The study area is situated in southern Siberia in the Russian Federation on the territory of the Altai Republic, along the borders with Kazakhstan, China and Mongolia. The area is situated between latitudes 49°10′ and 49°55′N and longitudes 86°50′ and 88°30′E. Geographically, the investigated region is delimited by the southern Chuya Range in the north, the Tarkhata mountain pass in the east, the Ukok Quiet Zone with the Tabon Bogdo Ula Mountain in the south, and the Koksu and Argut River valleys in the west (Fig. 1). The main part of the research was conducted during the summer seasons of 2003 and 2004.

The area is characterized by grass–sagebrush steppes and to a lesser extent by larch taiga and dwarf birch shrubs, with marsh, streams and lakes, surrounded by high mountain ranges. Elevation ranges from 1200 to 4120 m a.s.l.; the forest line is at about 2200–2300 m a.s.l. The vegetation season lasts *c*. 130 days (Sanheim, 2003). The region represents a complete sequence of altitudinal vegetation zones

Table 1 Potential explanatory variables used to characterize the habitat of *Spermophilus undulatus*

Variable	Description
(1) Environment	
Altitude	Altitude (in metres above sea level) (limits: 1231–2978)
Slope	Degrees (limits: 0–45)
Exposition	Exposure to sun, ordinal scale: (1) N, (2) NW or NE, (3) W or E, (4) SW or SE, (5) S
Water distance	Distance from nearest water resource (in metres) (limits: 0–1500)
Geomorphology	Factorial variable: (1) steppe (grassland), (2) rocky steppe, (3) river valley, (4) lake shore, (5) boreal forest (taiga), (6) alpine steppe (semi-arid), (7) alpine valley (semi-humid), (8) mountain hill, (9) mountain slope, (10) plateau
(2) Management	
Human disturbance	Ordinal scale: (1) low, (2) medium, (3) high
(3) Vegetation	
Herb cover	Presence of herbs (non-woody vegetation usually up to 50 cm of height) in per cent (limits: 2–100)
Bush cover	Presence of bush (woody vegetation up to 2 m of height) in per cent (limits: 0–90)
Tree cover	Presence of trees (woody vegetation more than 2 m of height) in per cent (limits: 0–80)
Plant community	Factorial variable: (1) pastures in valleys, (2) mountain meadows, (3) larch taiga, (4) slope debris, (5) shrubby veg. domin. by *Betula rotundifolia,* (6) wetland veg., (7) short-grass steppe with rare shrubs, (8) short-grass steppe, (9) short-grass tundra-steppe, (10) tundra-steppe in alluvia, (11) shrubby veg. domin. by *Potentilla fruticosa* and *Salix* sp., (12) arid steppe veg. with shrubs, (13) alluvial tree veg., (14) alpine shrub veg.
Height of herbs	Ordinal scale: (0) $<$10 cm, (1) 10–25 cm, (2) $>$25 cm
(4) Geology	
Stone cover	Presence of stones in per cent (limits: 0–90)
Soil	Factorial variable: (1) chernozem, (2) brunisol, (3) luvisol, (4) podzol, (5) regosol
Soil thickness	Ordinal scale: (0) no soil, (1) $<$0.1 m, (2) 0.3–0.1 m, (3) 0.5–0.3 m, (4) $>$0.5 m
Surface geology	Factorial variable: (1) loess, (2) clay, (3) sand, (4) gravel, (5) bedrock schists, (6) bedrock granite
% of coarse clastics	Ordinal scale: (1) $<$10%, (2) 11–30%, (3) 31–49%, (4) 50–69%, (5) $>$70%
Relative surface humidity	Ordinal scale: (1) arid, (2) semi-arid, (3) semi-humid, (4) humid
(5) Other species	
Marmota spp.	Presence or absence of *Marmota baibacina* in the plot
Ochotona spp.	Presence or absence of *Ochotona alpina/pallasi* in the plot

from semi-desert, steppe, forest-steppe, taiga, to sub-alpine and alpine-tundra.

Climate is strongly continental. The average July temperature in the Chuya steppe is $+25\,^{\circ}$C, whereas the average January temperature is $-33\,^{\circ}$C. Climatic conditions in the mountains are generally less severe than in the open steppes, and a microclimate prevails throughout the year in some protected locations in the Altai Mountains. The cyclic nature of the glacial and interglacial periods led to periodic landscape transformations and the generation of specific ecosystems adjusted to particular topographic settings and responding to climatic variations. Most of the area is underlain by perennial permafrost with the active thaw layer 30–70 cm thick (Chlachula, 2001).

Precipitation rates as well as annual temperatures vary greatly according to the particular topographic setting. Most of the precipitation falls on the W/NW slopes (600–800 mm year^{-1}). The Plateau Ukok (2300–2500 m a.s.l.) represents a semi-arid region (precipitation *c.* 200 mm year^{-1}) with very low mean annual temperatures ($-10\,^{\circ}$C) and xenotheric vegetation (Rudoy *et al.*, 2000).

The 'Ukok Quiet Zone', covering over half of the research area, is one of several areas that make up the 'Golden Mountains of Altai' UNESCO World Heritage Site created in 1998. This area was granted nature park status in October 2005. Traditional extensive livestock raising is the major form of land use. Overgrazing represents an important problem in wildlife conservation and ecological management planning.

Data collection

A total of 51 transects was established in a random order to cover most of the habitat's heterogeneity. The length of each transect was *c.* 1 km. Along these transects, 309 plots of 50×50 m were established at 200 m intervals (following Allainé, 1994). The ecological parameters estimated in each plot were assigned to five categories: (1) environment, (2) management, (3) vegetation, (4) geology and (5) other burrowing mammalian species (Table 1). Each plot was thoroughly checked for the presence of burrows of ground squirrels, marmots and pikas. Active burrows were differentiated from old and inactive ones by the presence of fresh soil deposits, faeces and runways. Only active burrow systems were included in the analysis. Some of the variables were entered in ordinal scale. The limits of classes were fixed prior to balance their biological significance.

Environmental features include altitude, slope, exposition, distance to the nearest water source and geomorphologic characteristics, described in Table 1 (for details see Supplementary Material Appendix S1). The presence of marmots (*Marmota baibacina* Kastschenko, 1899) and pikas (*Ochotona alpina* Pallas, 1773 and *Ochotona pallasi* Gray, 1867) in each plot was also recorded to estimate the possible influence of interspecies competition in respect to habitat use of the long-tailed ground squirrels.

Plant cover is the proportion of the plot covered by herbs and grasses, shrub or trees, respectively. The height of herbaceous cover is divided into three categories reflecting the height of the adult ground squirrel (*c.* 30 cm; Gromov & Erbayeva, 1995). Plant communities (see the Supplementary Material Appendix S1) were originally estimated to describe the geographically extensive and

Table 2 Effects of single variables and best models on the occurrence of *Spermophilus undulatus*

Model	Direction	Residual deviance	d.f.	AIC	*F*	*P*
Null		333.10	308	334.45		
Null + Transect		193.53	50 258	259.98	4.28	***
Environment						
Altitude		191.99	1257	259.74	2.36	NS
Slope	+	189.76	1257	259.63	5.60	*
Exposition		193.50	1257	262.22	0.04	NS
Water distance[a]	±	182.42	2256	251.90	8.47	***
Geomorphology	[b]	179.82	10 248	263.71	1.99	NS
Water distance[a] + slope		179.18	1255	250.08	4.93	*
Management						
Human disturbance	+	191.53	1257	259.29	3.07	NS
Vegetation						
Herb cover[a]	±	180.04	2256	246.73	10.72	***
Bush cover[a]	−	181.40	2256	247.31	9.75	***
Tree cover	−	188.97	1257	255.86	7.08	**
Height of herbs	−	179.21	1257	247.41	21.83	***
Plant community	[c]	162.97	13 245	238.73	3.97	***
Height of herbs + herb cover[a]		170.42	2255	240.60	6.76	**
Height of herbs + herb cover[a] + bush cover[a]		164.99	2253	237.98	4.17	*
Geology						
Stone cover		192.20	1257	262.09	1.97	NS
Soil type	[d]	185.30	5253	256.80	2.58	*
Soil thickness	−	184.73	1257	251.70	13.67	***
Surface geology	[e]	168.63	7251	242.95	5.55	***
% of coarse clastics[a]	±	188.80	2256	257.29	3.66	*
Relative surface humidity	−	188.11	1257	254.21	8.52	**
Other species						
Marmota spp.		192.61	1257	261.84	0.24	NS
Ochotona spp.		193.53	1257	262.32	0.99	NS
Best model-combined variables						
Height of herbs + surface geology + water distance[a] + bush cover[a] + soil thickness		122.50	2243	196.16	5.86	**

Direction means how the variable affects the distribution, and is shown only in significant results. Values in more complex models refer only to their previous model.

*$P<0.05$.

**$P<0.01$.

***$P<0.001$.

[a]Polynomial relationship of dependent variable.

[b]Only in steppe, rocky-steppe, alpine meadows and mountain steppes, absent in lake shores.

[c]Pastures, short-grass steppe, short-grass tundra-steppe and alluvial tundra-steppe.

[d]Mainly chernozem.

[e]In loess, sand on bedrock schists, bedrock schists and bedrock granite.

AIC, Akaike information criterion; NS, not significant.

biologically heterogeneous study area in relation to ground squirrel habitat use.

We recognized three categories of human disturbance (high, medium and low). Human disturbance was considered high when the plot contained evidence of human activity (e.g. tracks or signs of intensive grazing by domestic livestock) and low when it did not.

Geology and soil characteristics are listed in Table 1. These variables describe soil composition, bedrock and surface cover composition (rock and stones distribution), and relative surface humidity of the plot. Soil characteristics were described according to the Expert Committee on Soil Survey (1987).

Data analysis

We analysed the data by general linear models (GLMs) using the S-Plus 2000 package (S-Plus 2000, 1999). This method allows analysis of dependent variables also with distributions other than Gaussian. For our computation, we used the dependent variable (presence or absence of ground squirrels on individual plots) with the binomial distribution. To delimit effects of space autocorrelation, we included the variable 'Transect' (where the individual plots were nested) to all models as a covariable. First, we included single variables from Table 1 to the 'Null + Transect' model and tested which variables gave significant results [using the Akaike information criterion (AIC) and *F*-statistics]. In the next computations, we used only the significant variables. We used the forward selection procedure for building more complex models. We included to the best model (significant results and lowest AIC) all variables chosen in the previous step, and repeated the procedure until the fit was not improved.

Results

Ground squirrels settlement occurred in 29 (56, 86%) of the 51 transects measured and in 70 (22.65%) of the 309 plots measured. The results are summarized in Table 2.

Effects of the vegetation variables

Ground squirrels significantly preferred areas without tree cover and tolerated only a small density of bush vegetation (up to 35%; Fig. 2b), whereas density of herbaceous cover represented a significant component in ground squirrel habitat choice, with an optimum between 40 and 70%.

Ground squirrels preferred plant communities dominated by *Poaceae*, *Potentilla* and *Artemisia*, without bush or tree cover (i.e. pastures in valleys, short-grass steppe, short-grass

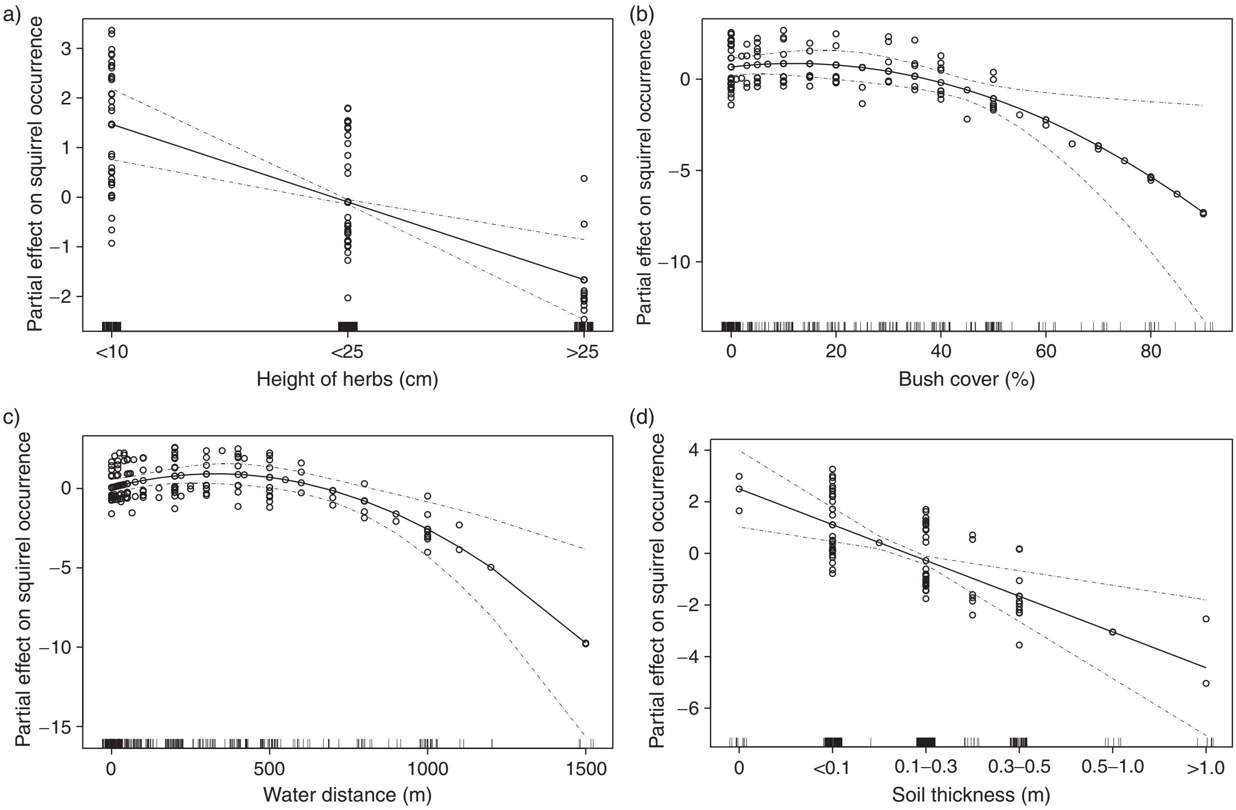

Figure 2 Effect of selected environmental, vegetative and geological variables on the occurrence of the long-tailed ground squirrel *Spermophilus undulatus* in the southern Altai Mountains: (a) height of herb cover; (b) density of bush cover; (c) water distance; (d) soil thickness. The broken lines represent 95% confidence intervals.

tundra steppe and alluvial tundra steppe). The height of herb cover was one of the most important factors influencing habitat use. They significantly preferred areas with a low herbaceous cover, optimally at about 10 cm of height (Fig. 2a). The amount of bush and herb cover, together with the height of herbs, represented the most important vegetation variables; ground squirrels selected habitat with only a small amount of bush cover and a medium amount of low herbaceous cover.

Effects of the environmental variables

Altitude and exposition did not significantly affect the ground squirrels' habitat preferences. Their colonies occurred more frequently on steep slopes ($>20°$) than on gentle slopes. Also, the distance to the nearest water source (stream, river or lake) significantly affected the probability of ground squirrel occurrence; they selected habitats *c.* 100–300 m far from the water source (Fig. 2c). Ground squirrels preferred steep slopes at a short distance to the water source.

Effects of the geological variables

A reduced soil thickness (10–30 cm) did not discourage ground squirrels from building burrow systems; they even displayed significant preferences for such habitats (Fig. 2d). They significantly more often built their burrows in soil with a higher amount (50–70%) of coarse clastics. The amount of stone cover did not significantly affect the probability of ground squirrel settlement.

Ground squirrels occurred significantly more frequently in loose wind-borne deposits (loess and sand) and above bedrock (disintegrated schists and granite blocks) than in wet clay or compact gravel. Chernozemic soils were significantly more preferred to other soil types. Relative surficial humidity is another factor affecting significantly the habitat selection of ground squirrels, which proffered arid and semi-arid areas.

Soil type, soil thickness, surface geology, amount of coarse clastics and relative surface humidity significantly affected the ground squirrels' habitat preferences. They selected arid and semi-arid habitats with a small layer of chernozem soil containing large amounts of coarse clastics and avoided subsoil layers composed of clay or gravel.

Effect of the management

Ground squirrels did not avoid areas with high human disturbance, and displayed a slight preference for the more disturbed habitats, although the effect was marginal (at $P=0.08$).

Effect of the other species

Neither the presence of pikas nor of marmot settlements in the plot had any impact on the habitat selection of ground squirrels.

The results of the analysis show five variables, the combination of which provides the best description of ground squirrel habitat: height of herbs, surface geology, water distance, density of bush cover and soil thickness (see Table 2 and Fig. 2a–d).

Discussion

The distribution of long-tailed ground squirrels in the southern Altai area is affected mainly by the height of herbaceous cover, distance to the water source, density of bush cover, soil thickness and the particular subsoil geological layer. Our results suggest that ground squirrels prefer dry and steep low-grass steppes, near the water source and with a thin layer of a chernozem soil containing large amounts of coarse clastics. The species strictly avoids forests and tolerates only a small density of bush cover.

Ground squirrels avoid clay and gravel soil, probably because of a lower water permeability of the former and the difficulty of burrow construction of the latter. Higher occurrences in areas with a lower soil thickness and a higher proportion of coarse clastics probably reflect their preference for arid and semi-arid habitats. Thick soil layers with small amounts of coarse clastics are typical for regularly flooded humid areas. Better drainage and reduced humidity are probably more important factors than higher energetic costs associated with burrow construction in hard stony soil (Gromov & Erbayeva, 1995; Ebensperger & Bozinovic, 2000). Moreover, good drainage prevents the formation of permafrost. It is impossible for the ground squirrels to dig through frozen soil.

The presence of pikas and marmots does not apparently affect the ground squirrel's habitat selection; the species probably does not compete over food or burrow sites. However, our results could be distorted by the fact that the marmots are frequently hunted and their distribution and habitat selection could be altered. Preferences for habitats with a medium density of very low herbaceous cover as well as a lack of interactions with other burrowing herbivores suggest that habitat selection of ground squirrels may be determined rather by burrowing conditions and predation risk than by food availability. However, food availability may limit density and overwinter survival, as in arctic gound squirrels (Karels *et al.*, 2000).

Predation risk may be influenced strongly by vegetative cover (Lima, 1990; Cassini & Galante, 1992). The cover can provide concealment from predators and obstacles to pursuing predators (Wywialowski, 1987). Conversely, it can obstruct an animal's view of its surroundings, shortening the distance at which the prey can detect predators visually (Carey & Moore, 1986; Ebensperger & Hurtado, 2005). Burrows of the arctic ground squirrels were located on sloped sites in open areas with high visibility (Karels & Boonstra, 1999). Ground squirrels generally rely more on their sight for predator detection than on other senses; therefore, they display preferences for a tabular habitat with a low vegetation cover.

The degree of human disturbance is not a significant factor affecting the distribution of ground squirrels. The species even seems to prefer heavily grazed habitats near human settlements and roads. Intensive grazing prevents shrubs and forest invasion, keeps the vegetation low and thus provides appropriate conditions for ground squirrels, favouring open settings where predators can be easily detected by sight. Tupikova (1989) mentioned that preferences for roadsides and banks of the irrigation ditches are typical for ground squirrels in the Altai Mountains. Human persecution, for example hunting or poisoning, was not observed in the study area. Some species, such as *Spermophilus tridecemlineatus* Mitchill, 1821, increased in range and numbers as forests were cleared and agriculture expanded (Nowak, 1999). In contrast, *Spermophilus franklinii* Sabine, 1822, has declined in response to destruction of its tall grass habitat because of agricultural and urban expansion (Johnson & Choromanski-Norris, 1992).

Altitude and exposure to sun do not represent significant factors in the habitat choice of *S. undulatus*. This choice may reflect adaptation of the species to the cold arctic environment, as the distribution area of the long-tailed ground squirrel reaches far north and borders with the arctic ground squirrel (*Spermophilus parryi* Richardson, 1825) (Panteleyev, 1998). For *S. undulatus* a relatively longer period of activity is typical, lasting usually from March to October (Gromov & Erbayeva, 1995). Lower annual temperatures, a higher snow cover and a shorter vegetation season in higher altitudes and northern slopes do not prevent ground squirrels from establishing settlements.

The species selected habitats at 100–300 m from the water source; preference for well-drained banks out of reach of spring floods was also found for arctic ground squirrels (Carl, 1971). A strong preference for the proximity of the water source may possibly prevent the species from colonizing vast steppes of Central Asia and may restrict the distribution to mountain areas.

Evolution of relationships between animals and their habitats may be strongly affected by stochastic events and historical contingency (Storch & Frynta, 1999). Habitat requirements of the ground squirrels differ strongly between the southern and northern parts of their distribution area. The northern relic populations occupy open forests, forest clearings and meadows with shrubs and a dense vegetation cover (Gromov & Erbayeva, 1995). In taiga, ground squirrels inhabit widely distributed single burrows, whereas in the Altai and Sayan grasslands the species lives in colonies of about 15 animals with a strict social hierarchy. A dominant male controls a territory covering *c.* 150 m^2 (Shilova *et al.*, 1979). Young males usually disperse at a distance of 2 km or more from their natal burrows (Gromov & Erbayeva, 1995).

A similar pattern has been shown for the arctic ground squirrel. The species has a higher population density in alpine meadows than in boreal forest (Karels & Boonstra, 2000) and arctic ground squirrels living at higher elevations have a higher reproductive output than their neighbours, inhabiting a low-elevation boreal forest (Gillis *et al.*, 2005).

Thus, the long-tailed ground squirrels contribute in many ways to the functioning of the mountain grassland ecosystem and possibly may represent a keystone species of the southern Altai steppes. In sum, the long-tailed ground squirrel shows a broad ecological valence and its populations are not endangered by the natural habitat disturbance caused by humans and domestic livestock.

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Supplementary material

The following material is available for this article online:

Appendix S1 Overview of plant communities and geomorphology variables used in analyses of habitat requirements of the long-tailed ground squirrel.

This material is available as part of the online article from http://www.blackwell-synergy.com

