

Habitat engineering under dry conditions: The impact of pikas (*Ochotona pallasii*) on vegetation and site conditions in southern Mongolian steppes

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Abstract

Question: Does ecosystem engineering by small mammals have a significant influence on vegetation patterns in the arid steppe vegetation of southern Mongolia?

Location: Gobi Altay Mountains, southern Mongolia.

Methods: We assessed the impact of the small lagomorph *Ochotona pallasii* on plant community composition, nutrient levels and biomass production in montane desert steppes. Data were derived from vegetation relevés, harvests of above-ground standing crop and a bioassay, followed by analyses of soil and plant nutrient contents.

Results: Although the local climate is arid with <150 mm annual precipitation, clear evidence of allogenic ecosystem engineering was found. Plant communities on burrows differed from those on undisturbed steppe in that they contained more species of annuals and dwarf shrubs, and a greater abundance of the important fodder grass *Agropyron cristatum*. Standing crop and nutrient concentrations were higher for plants growing on burrow soil. *In situ* measurements and a pot experiment showed that this effect was related to increased levels of soil nutrients (P, K, N) rather than moisture availability.

Conclusions: The study confirms that *O. pallasii* positively influences soil nutrient levels on its burrows, which leads to increased grassland productivity even under dry conditions. Thus, *O. pallasii* does not deteriorate site conditions, and the need for presently applied pest control schemes aimed at this species should be reassessed.

Keywords: Allogenic engineer; Arid environment; Nutrient; Plant community composition; Soil; Small mammal.

Nomenclature: Scientific names of plants follow Grubov (2001).

Introduction

The importance of small mammals to the ecology of arid and semi-arid regions represents one of the crucial issues for such environments. They have a direct impact on the vegetation through herbivory and seed dispersal, but also alter the site conditions (Kinlaw 1999; Whitford & Kay 1999). Burrows often show increased soil nutrient concentrations, lower bulk density and increased water infiltration. Thus, burrowing small mammals modulate resources utilized by other species, and are often regarded as prime examples of 'ecosystem engineers' (Jones et al. 1994). This concept has been widely and critically discussed (Power et al. 1996; Reichman & Seabloom 2002; Wilby 2002; Wright & Jones 2006). One important result is that the relative importance of ecosystem engineering by a given species depends on the site conditions including productivity and climate (Crain & Bertness 2006; Kotliar et al. 1999; Wright & Jones 2004). Here, we present data collected under strongly arid conditions, where ecosystem engineering has, as yet, rarely been studied.

Most examples of ecosystem engineering by small mammals come from North America (e.g. Fahnestock & Detling 2002; Kerley et al. 2004; Kotliar et al. 1999; Miller et al. 1994), while information from other regions is scarce. In Asia, rodents and lagomorphs are widespread in all steppe types ranging from relatively moist forest steppes and meadow steppes in Siberia (Zlotin & Khodshova 1980), to arid desert steppes in Mongolia (Breymeyer & Klimek 1983; Weiner et al. 1982a). Several species are known to alter soil conditions and promote the growth of less palatable plant species. Such observations have triggered a vigorous discussion on their potential status as pest species, and whether or not they should be controlled by large-scale poisoning (Smith & Foggin 1999; Zhang et al. 2003a; Zhang et al. 2003b).

Precipitation regimes are assumed to influence the effects of small mammal burrowing (Jones et al. 1997). Thus, although enhanced nutrient availability on burrows can even occur under relatively dry conditions (<300 mm annual precipitation, Weiner et al. 1982a), ecosystem engineering by burrowing rodents should be relatively unimportant in dry regions, as the governing factor (water) is beyond their control. Surprisingly, very few studies have been carried out on dry grasslands with less than 200 mm annual precipitation (Kerley et al. 2004).

We examined the impact of small mammals on a dry grassland with <150 mm annual precipitation in southern Mongolia. Specifically, we asked the following questions: (1) Do small mammals affect vegetation in terms of community composition, richness, and biomass production? And, (2) are possible differences related to altered abiotic resources including water availability?

The results are discussed with respect to the impact of small mammals on rangeland quality, which is important for the prevailing pastoral land use.

Material and Methods

Study area

The study site in southern Mongolia is part of the Gobi Gurvan Saykhan National Park (43°36.949'N, 103°46.450'E), but virtually the entire region is under permanent livestock grazing (Stumpp et al. 2005). The site is located on the upper pediments of the Gobi Altay at 2200 to 2300 m asl with a southern exposure and shallow inclination (3–6°). Burozems constitute the dominant soils that have developed on deep deposits of silt and fine sand interlaced with occasional layers of scree. Regosols are restricted to active erosion gullies and scree slopes (Wesche et al. 2005).

Bayandalay, a governmental weather station (30 km SW of the study area at 1500 m asl), reports a long-term mean annual temperature of 4.5°C (January –18°, July 20°C), while mean precipitation is 110 mm with a high coefficient of variation (~35%; data National Meteorological Service). Precipitation increases with altitude and short-term measurements around the study site indicate higher, but equally variable, precipitation levels (Retzer et al. 2006). Most of the precipitation falls in summer; dew is extremely rare and does not contribute to moisture availability.

Montane steppes with *Stipa krylovii*, *S. gobica* and *Allium polyrrhizum* represent the dominant vegetation (Wesche et al. 2005) at the study site, which is typical for the upper pediments in the region according to a large-scale vegetation survey (von Wehrden et al. 2006;

Wesche et al. 2005). These steppes represent the most important pastures in the region, and are intensively used by both domestic livestock and small mammals. Pikas (*Ochotona* spp.) are the most important small mammal group (Nadrowski 2006) and their burrows are easily recognized in the field by their different vegetation and topsoil texture (Komonen et al. 2003). Two burrow types are distinguished with either the dominance of dwarf shrubs (mainly *Artemisia santolinifolia*), or the dominance of grasses (mainly *Agropyron cristatum*). The latter are common on the slightly sloping pediments, while those with *Artemisia santolinifolia* are restricted to coarse soil substrates along erosion gullies or at the foot of scree slopes.

Study species

Ochotona pallasi (Lagomorpha) is the most common small mammal in the montane steppes of the GGS NP. It occurs between 2200 – 2800 m asl in the steppes described above and has an estimated minimum total range of ca. 600 km² in the GGS NP (spatial data by von Wehrden et al. 2006). Pika build relatively stable populations of 10–30 animals per ha (Nadrowski 2006). Burrows are inhabited by single individuals, and abandoned burrows are soon occupied by other individuals. They occupy 7 – 12% of the surface area in the study region and are regularly distributed in space. They range in size from 4.5 to 108 m², some 10% of which comprise entrances. Burrows are thus large structures, suggesting that they last several decades or more (Whitford & Kay 1999). During a 4 year period (2000–2005) we did not observe a single new burrow being dug. Pikas are prime excavators (allogenic engineers, Kinlaw 1999) and central-place foragers.

Data collection

In July 2002, we randomly selected 12 burrows on three different pediment areas (maximum separation 1 km) from each burrow type (henceforth called *Artemisia* burrows and *Agropyron* burrows). Vegetation was recorded in 3 m × 3 m relevés on burrows and adjacent intact steppe. Plant cover estimates were cross-checked against point-intercept-frame measurements on *Agropyron* burrows (6 m² on each burrow and steppe), which indicated the same differences (data not described). Measurements of soil conditions concentrated on the topsoil (depth 3–10 cm), because this is the layer of maximum root concentration (Borisova & Popova 1985). We used a Theta Probe (Delta T-Instruments) to record volumetric soil water content of the topsoil as the mean of three instantaneous measurements on any given plot. Measurements were taken directly after one

of the few heavy rains (July 2003), and repeated after 10 days of total drought. Readings were calibrated for local soil texture. In August, mixed soil samples were collected within the relevés; samples were taken at least 40 cm away from dwarf shrubs, and at least 5 cm away from herbaceous perennials.

Soil was analyzed for a set of parameters expected to affect plant growth. Soil pH and conductivity were measured in water (20 g dry fine soil, 50 ml H₂O, probe SenTix 21, WTW, Germany); total carbon and nitrogen was measured with a CN-Analyser (Vario EL, ELEMENTAR, Germany). Nitrate and ammonium were extracted with 1 M KCl and subsequently determined with ICP. Cations were extracted with NH₄Cl (0.1 mol/l); Ca and Mg were analyzed with atomic absorption spectrometry; and K and Na with flame spectrometry (Flame AAS Vario EL, Analytik Jena, Germany). Available phosphate was extracted with Ca-Lactate at pH 3.6 and measured with a photometer (EPPSTEIN, Germany). Total carbon figures were corrected for carbonate-borne C measured with HCl (10%). All data refer to dry (105°C) fine soil (< 2mm).

Differences in productivity under unlimited water supply were assessed in a bioassay experiment because *in situ* watering seemed infeasible due to the large point to point variability of water infiltration on burrows. As the dominant species were slow growing perennials, which are difficult to establish from seeds and not easily transplanted, we used commercially available seeds of *Raphanus sativus sativus*. Five seeds were planted in June in 1 litre of mixed topsoil collected at the sampling sites described above and passed through a 2 mm sieve. Pots were exposed to ambient temperature, but placed under canvas to avoid radiation exposure. Water was added *ad libitum* until plants were harvested in August. Shoots were oven-dried (105°C) and mean weight of dry shoots per pot was used as a proxy for productivity under unlimited water supply.

Agropyron cristatum was the main fodder grass in our area (Jigjidsuren & Johnson 2003), so *Agropyron* burrows were studied in more detail. We measured above-ground standing crop on 12 *Agropyron* burrows and on adjacent controls in 2-4 m distance. Standing crop was harvested from within small grazing-proof cages 0.3 m² in size (cf. Zlotin & Khodshova 1980). Biomass was cut 2 mm above the surface covering the entire cage except its edges (subsample size 0.25 m²). Cages were harvested in August 2002 and in July and August 2003; data from July and August 2003 were summed up to estimate production over one year. Cages were randomly placed on the steppe, but this was not possible on burrows as entrances had to be avoided. Non-random placement of cages on burrows may lead to confounding effects as cages could have had unrealistically high

initial cover values. Thus, cover at the initiation of the experiment was used as a covariate in data analysis to avoid a possible bias (see analysis).

Oven-dried biomass (105°C) served as a proxy for productivity. For some samples which became mouldy, oven-dried biomass was extrapolated from air-dried biomass using relationships that had been established for the intact samples. We analyzed samples from the bioassay and biomass harvested on burrows and steppe for nutrient contents. Oven-dried biomass was ground prior to analysis; total N content was determined with the described CN-Analyser; for Ca, Mg, K and P contents, organic matter was digested with hot HNO₃ and then processed in the same manner as described for the soil samples.

Data analysis

Detrended Correspondence Analysis was used to analyze differences in vegetation cover data. Because DCA indicated that vegetation differed among burrow types, two separate Redundancy Analyses were calculated to assess the relation between vegetation and site conditions (ter Braak & Šmilauer 2002).

For normally distributed variables (Kolmogorov-Smirnov-Test, percentages arc-sin transformed), univariate comparisons among burrows and controls were performed with *T*-tests for paired samples; in two cases we used non-parametric Wilcoxon tests. The effect of *Agropyron* burrows on annual biomass production (estimated by dry standing crop) was analyzed using a linear mixed effect model (Pinheiro et al. 2006). Blocks of burrow site vs. adjacent steppe constituted the random factor, while initial cover was used as a covariate. The full model also included habitat (burrow vs. steppe) as a fixed effect and the interaction between cover and habitat. This model was first reduced by excluding the interaction and then by removing habitat itself. Models were compared using likelihood-ratio tests. Due to a missing value on a burrow plot, we used 23 observations on 12 burrow-steppe groups. For estimation of the habitat effect, initial cover was set constant to 8%, which is intermediate between steppe and burrow plots.

Multivariate analyses were performed using CANOCO 4.5 and CANODRAW 4.0 (ter Braak & Šmilauer 2002); univariate statistics were calculated with SPSS 12.0 (Anon. 2003) and "R" (Anon. 2004). Significances refer to uncorrected type 1 errors because our study had an exploratory character (Roback & Askins 2005).

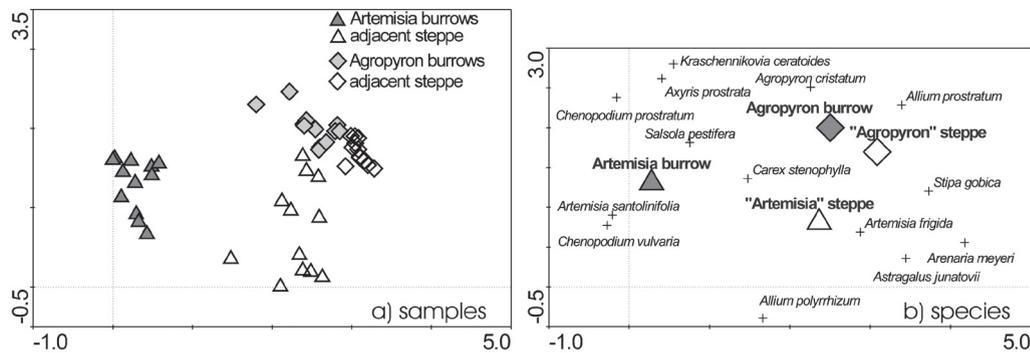


Fig. 1. DCA of the 48 vegetation samples (species log {x+1} transformed; detrending by segments; downweighting of rare species). Eigenvalue/length of gradient axis 1: 0.72/3.28 SD; axis 2: 0.27/2.46; axis 3: 0.14/1.709). (a) Plot of samples; symbols indicate origin of the given sample (\blacktriangle = *Artemisia* burrow, \triangle = adjacent steppe; \blacklozenge = *Agropyron* burrow, \lozenge = adjacent steppe). (b) Plot of species; only the 14 species best represented by the ordination are shown (weight >5%). The larger symbols (centroids) indicate mean position of the samples of a given group to facilitate comparison with Fig. 1a.

Results

Plant community composition

The DCA revealed clear differences between plant community composition on Pika burrows and on the surrounding steppe, but also among burrow types (Fig. 1a). Controls adjacent to *Agropyron* burrows formed a closed group, while steppes adjacent to *Artemisia* burrows were scattered in the ordination space (Fig. 1a). The ordination of species (Fig. 1b) indicates that the annual species *Chenopodium vulvaria*, *C. prostratum* and *Salsola pestifera* characterize *Artemisia* burrows, while *Agropyron* burrows share most of their species with the surrounding steppe.

Total species richness on *Artemisia* burrows, was significantly lower than on the controls (Fig. 2a). Only

dwarf shrubs and annuals had more species on burrows, while all other life forms most notably perennial herbs and grasses, were richer in species on the steppe (Fig. 2a). Richness of annuals was also much higher on the *Agropyron* burrows compared to the controls, while differences in numbers of perennial species were relatively small. This resulted in an overall increased species richness on the burrows. Total cover on *Artemisia* burrows was higher than on the controls (paired *T*-test, $n = 12$, $p < 0.001$). This was related to a much higher cover of *Artemisia santolinifolia* and of annual species, while *Agropyron cristatum*, *Stipa* spp. and *Allium* spp. were more common on the controls. Total cover was also higher on *Agropyron* burrows compared to the adjacent steppe ($p < 0.001$), due to higher values of *Agropyron cristatum* and the annual species.

Table 1. Summary of soil conditions on burrows compared to the immediately adjacent steppe. Only variables related to vegetation patterns according to an RDA were tested (mean; SD in brackets; $n = 12$; *T*-tests for paired samples, ^W = significance based on Wilcoxon test; (*) = $p < 0.06$; * = $p < 0.05$; ** = $p < 0.01$).

	a) <i>Artemisia</i> burrows				b) <i>Agropyron</i> burrows					
	burrow		steppe		burrow		steppe			
% C	2.94	(0.63)	2.29	(0.54)	**	2.38	(0.24)	2.33	(0.21)	ns
% N	0.66	(0.07)	0.61	(0.07)		0.59	(0.06)	0.62	(0.07)	
NO ₃ (mg/100g)	2.33	(1.26)	0.35	(0.50)	**	1.17	(1.22)	0.46	(0.73)	^W *
NH ₄ (mg/100g)	0.68	(0.25)	0.73	(0.25)		0.68	(0.17)	0.49	(0.17)	*
P (mg/100g)	5.86	(4.25)	1.99	(2.43)	(*)	2.37	(1.39)	0.85	(0.29)	**
K (g/kg)	0.30	(0.13)	0.15	(0.04)	**	0.22	(0.05)	0.18	(0.11)	
Ca (g/kg)	2.02	(0.29)	2.30	(0.35)	*	2.30	(0.33)	2.71	(0.28)	**
Mg (g/kg)	0.34	(0.07)	0.34	(0.04)		0.27	(0.06)	0.36	(0.05)	**
Conductivity (μ° S)	206.3	(84.0)	132.3	(61.0)	ns	205.8	(48.8)	149.6	(5.1)	*
Vol% H ₂ O (dry cond.)	0.7	(0.88)	3.2	(1.51)	**	2.9	(1.49)	4.5	(2.86)	
Vol% H ₂ O (wet cond.)	17.7	(4.72)	19.5	(2.63)	ns	13.4	(5.25)	15.6	(4.03)	

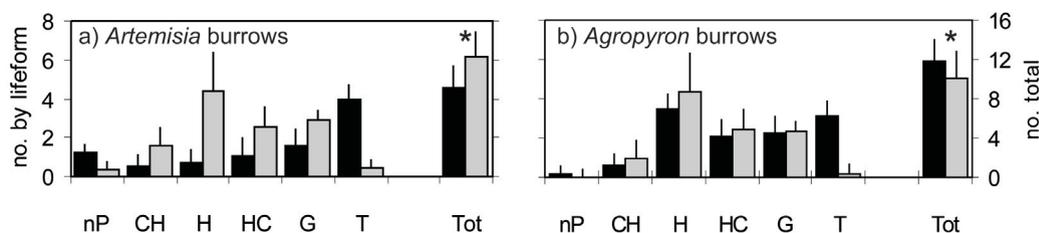


Fig. 2. Mean species richness of the two burrow types in comparison to the adjacent steppes (■ = burrow, ■ =steppes). Figures are given separately for major life forms (nP = Nano Phanerophytes, CH = Chamaephytes, H = Hemicryptophytes excl. grasses, HC = caespitose Hemicryptophytes, G = Geophytes, T = Therophytes; Tot = total species richness). Differences were tested for total species richness only (*T*-test for paired samples, *n* = 12). Error bars give 1 SD.

Soil characteristics

Monte Carlo tests (999 runs) on the first axes of the two Redundancy Analyses were significant at *p* < 0.05, and patterns resembled those revealed in the DCA. The first axes in both RDA ordinations separated burrows and non-burrow plots (*Artemisia* burrows: eigenvalues/cumulative variance in species data for axis 1: 0.46 / 46.3%, axis 2 0.12 / 12.1%; *Agropyron* burrows axis 1 0.41 / 40.8%, axis 2 0.17 / 17.2%). Vegetation on *Artemisia* burrows was correlated to higher levels of conductivity, higher contents of C, NO₃⁻, P, K, and lower water contents; when compared with the controls. Vegetation on *Agropyron* burrows was related to higher values of conductivity, C, NO₃⁻, NH₄⁺, P, and to lower values of Ca and Mg. These variables were selected for pair-wise tests of soil data (Table 1a).

Compared to the adjacent steppe, soils from *Artemisia* burrows had significantly higher contents of C, NO₃⁻, K and Ca; and to a certain extent P. Soil moisture was similar for both sites following rain, but after 10 dry days

top soils on the *Artemisia* burrows were significantly drier than those of the steppe. On *Agropyron* burrows contents of P, NO₃⁻, NH₄⁺ were somewhat lower than on *Artemisia* burrows but significantly higher than on the respective controls (Table 1b). Soil conductivity was also significantly higher on burrows, while Ca and Mg were slightly higher on the steppe. Differences in water content were not significant. Samples from unreplicated soil profiles produced a similar pattern and showed that differences among burrows and controls were restricted to the topsoil (up to 40 cm in depth).

Results from the bioassay

An average of 3-4 plants survived the 7 weeks of the experiment, with treatment affecting neither the number of radish plants (Table 2), nor the proportion of above-ground versus below-ground biomass. Pooled above-ground biomass was significantly higher on soils from burrows than on those from the respective controls, and the differences remained when data were standard-

Table 2. Results of the bioassay conducted with *Raphanus sativus sativus* grown in soil from the two burrow types and the adjacent steppes: Values for total mean number of plants per pot (5 seeds), percent above-ground biomass of total (wet) biomass, and total dry, above-ground biomass per pot. Nutrients were analyzed in mixed samples from all plants grown in a given pot (*T*-test for paired samples, *n* = 12, SD in brackets; * = *p* < 0.05; ** = *p* < 0.01; *** = *p* < 0.001).

	a) <i>Artemisia</i> burrow		adjacent steppe		b) <i>Agropyron</i> burrow		adjacent steppe			
Mean no. of plants	3.3	(1.7)	3.2	(1.6)	ns	3.6	(1.4)	3.8	(2.1)	ns
% aboveground biomass	21.92	(9.07)	20.67	(10.68)	ns	24.69	(7.11)	29.43	(14.03)	ns
Total aboveground biomass (g)	1.37	(0.74)	0.81	(0.57)	*	1.02	0.27	0.70	(0.34)	*
% N	3.87	(0.80)	2.96	(0.42)	*	3.88	(0.58)	2.99	(1.15)	*
Ca (g/kg)	43.66	(7.31)	53.63	(8.62)	*	53.83	(5.99)	56.73	(5.92)	ns
Mg (g/kg)	6.14	(1.11)	8.14	(1.88)	*	7.26	(1.62)	8.49	(1.43)	ns
K (g/kg)	23.67	(9.10)	16.28	(5.15)	*	23.29	(6.16)	18.46	(2.30)	*
P (g/kg)	2.49	(0.49)	1.51	(0.27)	***	1.85	(0.49)	1.47	(0.48)	ns

Table 3. Mean nutrient contents for the three dominant plant species *Agropyron cristatum*, *Allium polyrrhizum*, and *Stipa gobica* growing on *Agropyron* burrows and the adjacent steppe (*T*-test for paired samples, SD in brackets, (*) = $p < 0.06$; * = $p < 0.05$).

	<i>A. cristatum</i> (n = 11)				<i>A. polyrrhizum</i> (n = 12)				<i>S. gobica</i> (n = 7)			
	burrow		steppe		burrow		steppe		burrow		steppe	
% N	3.08	(0.23) (*)	2.73	(0.34)	3.33	(0.31)	3.22	(0.27)	2.51	(0.47)	2.31	(0.38)
Ca (g/kg)	4.04	(1.56)	8.94	(10.19)	9.51	(2.17)	12.64	(10.49)	4.51	(1.66)	9.98	(15.77)
Mg (g/kg)	2.06	(0.70)	1.74	(0.39)	3.62	(1.12)	3.85	(1.07)	1.38	(0.37)	3.16	(3.37)
K (g/kg)	17.20	(3.06) *	13.91	(3.99)	25.08	(6.46)	24.37	(4.22)	14.42	(18.17)	5.31	(1.11)

ized to the number of surviving plants (data not shown). Radish growing on soils from *Artemisia* burrows had significantly higher contents of N, K, and P; and lower contents of Ca and Mg than the respective controls. Similarly, radish growing on soils from *Agropyron* burrows showed significantly elevated contents of N and K (values for P were higher but not significant).

Plant nutrient contents and standing crop on Agropyron burrows

Nutrient content differed among important fodder plants growing *in situ* on *Agropyron* burrows and steppes (Table 3). Total contents of foliar N and K were higher on burrows, but differences were only significant for *Agropyron cristatum*. Calcium and Mg showed no clear trends.

There was no evidence that the effect of burrow vs. steppe habitat on standing crop production depended on vegetation cover at the beginning of the experiment ($df=1$, likelihood-ratio = 0.10, $p = 0.75$). The burrows showed higher production than the steppe habitat ($df = 1$, likelihood-ratio = 20.07, $p < 0.001$). Based on 8 % cover, the linear model gave estimates for the standing crop produced within one year of 1017.4 (± 258.6 SE) kg/ha for *Agropyron* burrows, and 453.6 (± 362.1 SE) kg/ha for the adjacent steppe.

Discussion

Are Pikas ecosystem engineers?

Pikas modulate the supply of abiotic resources used by other species and thus qualify as ecosystem engineers (Jones et al. 1994). Their burrows offer special site conditions leading to differences in plant community composition, vegetation cover, species richness and, at least for the *Agropyron* burrows, higher standing crop. Foliar nutrient contents are increased on burrows, and higher N-levels hint at higher contents of protein and possibly increased fodder quality. In particular, *Agropyron cristatum*, a grass preferred by livestock

(Jigjidsuren & Johnson 2003; Retzer 2007), benefited from the burrow habitat; this was also found on other sites in Central Asia (Hongo et al. 1993). The RDA implied that differences in the vegetation are related to soil conditions. Water contents tended to be lower under burrow vegetation, but levels of the crucial plant nutrients P and K were higher, while various fractions of N did not show such a clear pattern. Enhanced levels of P and K are often reported for small mammal burrows (Whitford & Kay 1999), while results for N are usually less clear and reflect its mobility in the soil.

Higher nutrient contents on burrows are usually seen as effects of small mammal activity, but there are at least two other possible explanations. (1) Pikas might have chosen nutrient-rich sites for their burrows: This seems unlikely with respect to the otherwise rather homogeneous soil conditions on the pediments and the regular spacing of the burrows. (2) Livestock grazing might be more intense on pika burrows (Smith & Foggin 1999) and faeces would add nutrients to the soil: We found no conclusive evidence for enhanced livestock grazing on burrows compared to steppe (Nadrowski 2006; Retzer 2004). We observed pikas concentrating dung on their burrows, but this supports the idea of allogenic engineering. The system can be seen as an example of “positive feedback engineering” (Jones et al. 1997) as pikas benefit from the increased fodder availability and improve their own living conditions.

These results confirm available studies on northern hemispheric small mammals (McIntyre & Hik 2002; Roach et al. 2001). In the dry regions of Central Asia *Microtus brandtii* is the most intensely studied species. At 150 - 250 mm annual precipitation, vole burrows show enhanced rain water infiltration and nutrient availability, and sometimes improved plant nutrient composition (Breymeyer & Klimek 1983; Weiner et al. 1982a). Voles trigger a succession towards less palatable plant species (Samjaa et al. 2000; Zhong et al. 1985), and this effect lasts after voles abandon their burrows (Weiner et al. 1982a). Burrows of the Tibetan *Ochotona curzoniae* host special plant communities with enhanced productivity, but also provide breeding opportunities for several animal species (Lai & Smith 2003; Smith &

Foggin 1999). Similarly, the bird *Oenanthe isabellina* nests in *O. pallasi* burrows in the GGS NP (pers. obs.). In Mongolia, effects of the widespread *O. daurica* are usually considered small when compared to those of *M. brandtii* (Komonen et al. 2003; Wang et al. 2003).

Ecosystem engineering under dry conditions

Annual plants benefit from disturbance and reduced competition by hemicryptophytes (Hilbig 1995), the same holds true for dwarf shrubs that grow preferentially on coarse and disturbed substrates (Wesche & Ronnenberg 2004). This is at least partly related to a moisture effect, due to greater water infiltration on small mammal burrows (Laundre 1993; Zlotin & Khodshova 1980), and shrubs tend to have deeper roots (Cheng et al. 2006; Li et al. 2004). Though we did not assess the specific mechanisms, fast drying of the topsoil on *O. pallasi* burrows (Table 1) suggests that pika activity also modulates the water availability.

Dry topsoils should have resulted in lower productivity on burrows, but we found increased standing crop in several species, most of which have shallow root systems. Our results suggest that soil nutrient content is responsible for this increase. The bioassay revealed that increased productivity and plant nutrient contents were independent from water availability, and trends were similar for *in situ* grown plants. High levels of foliar-N have also been described for North American small mammal colonies (Cid et al. 1991; Fahnestock & Detling 2002), but levels of foliar-N were much lower in studies from northern China (Yuan et al. 2005) and central Mongolia (Weiner et al. 1982b). Considerably lower soil-N concentrations on burrows and steppes (0.21% vs. 0.13%, Weiner et al. 1982a) explain these differences.

The apparent importance of nutrient concentrations is in contradiction to the idea that communities switch from nutrient limitation to water limitation below a certain limit of precipitation (i.e. 150 – 200 mm, cf. Hooper & Johnson 1999; Whitford 2002). Unfortunately, few studies are available on nutrient limitation in arid grasslands (< 200 mm). Most fertilization experiments in mid-latitude grasslands were performed at 300 mm annual precipitation or more (Gutierrez et al. 1988; Paschke et al. 2000). However, effects of fertilizer treatment differed among species in a Californian desert at 163 mm precipitation (Drenovsky & Richards 2004), but at least one species showed increased growth and foliar-N concentrations under NPK-fertilization, irrespective of the irrigation treatment. In central Mongolia, vegetation on nutrient-rich vole burrows showed enhanced productivity and foliar nutrient levels at 150 – 250 mm precipitation (Weiner

et al. 1982a). N-fertilization of desert steppes north of our study area resulted in increased productivity at 90 – 165 mm annual precipitation (Slemnev et al. 2004), and tentative results of a recently initiated NPK-fertilization experiment in our study site point in the same direction (Wesche & Ronnenberg unpubl.). Nutrient limitation in deserts is regarded to be largely caused by low levels of nitrogen (Hooper & Johnson 1999; Krueger-Mangold et al. 2004; Whitford 2002), and central Asian deserts are known for their low number of nitrogen-fixing legumes (Lavrenko & Karamysheva 1993). Phosphate concentrations were also low in our study region, and phosphorus may also be another limiting factor in desert regions (Drenovsky & Richards 2004; James et al. 2005)

Central Asia is characterized by a highly continental climate, where thermal conditions restrict the growing period to a few summer months that coincide with the main rainy season. Consequently, the percentage of precipitation effectively available for plant growth is higher than in less continental climates. This might explain why we found an example of allogenic engineering under drier conditions than other studies.

Do pikas change pasture quality?

Pika burrows covered up to 12% of the study area. Top soil P contents on burrows were three times as high as on the steppes, which leads to a crude estimate of some 25% increased P on the scale of the pediment. However, there is no evidence that pikas add nutrients to the system by transporting nutrients from lower soil layers upwards (P, K), or hosting more legumes on their burrows (N). Instead, their impact is most likely on nutrient redistribution and facilitation of decomposition (Whitford 2002). Scale of nutrient redistribution by herbivores is related to their activity radius: Large herbivores generally produce larger and thus more patchily distributed dung deposits, while small mammals distribute their faeces more locally (Bakker et al. 2004). Pikas move on a scale of a few metres and concentrate fodder, their faeces, and also dung of livestock on their burrows. Densities of the latter are up to 70-times higher on burrows than on steppe (Retzer 2004). In contrast, livestock facilitate a large-scale (10^2 to 10^3 m) nutrient translocation from the steppes to the vicinity of the few permanent wells and herder's camps, where animals defecate more (Stumpp et al. 2005) but productivity is low due to heavy trampling. This effect, coupled with the ancient and still widely practised tradition of using droppings as main fuel source, suggests that most steppe sites have been subjected to centuries of nutrient depletion. Pikas apparently counteract this loss and thereby conserve

nutrients on their burrows.

Burrowing activity is often thought to contribute to lasting steppe degradation in terms of soil conditions and fodder palatability (Lai & Smith 2003), in which case burrowers could be regarded as pest species. In contrast, our study found evidence for improved site and fodder conditions on pika burrows (higher standing crop, higher leaf nutrient contents). Existing large-scale poisoning schemes aimed at preventing long-term pasture degradation (Smith & Foggin 1999; Zhang et al. 2003a; Zhang et al. 2003b) thus seem inappropriate in the case of *Ochotona pallasi*.

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