## Facts from a year of drought:

# Forage competition between livestock and the Mongolian Pika (*Ocho-tona pallasi*) and its effects on livestock densities and body condition<sup>1</sup>

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## Abstract

Burrowing small mammals in grasslands have long been regarded as pests because they compete for forage with livestock and reduce the forage availability for livestock by destroying pastures through their intensive digging activity.

In order to investigate forage competition between the Mongolian Pika (*Ochotona pallasi*) and livestock an exclosure experiment consisting of four different treatments was set up. The treatments were: 1) accessible only for pikas, (*only pika*) 2) accessible only for livestock, (*only livestock*) 3) accessible for both herbivore groups (*pika & livestock*) and 4) no grazing (*no grazing*). During the investigation period all requirements for forage competition, namely overlap of habitat use, overlap of forage use, and forage scarcity were met.

The results of the exclosure experiment show that in the year of this study pikas consume a higher percentage of the vegetation than livestock does. Therefore, pikas are competitively superior to livestock. Nevertheless, both groups can coexist as they have access to mutually exclusive forage resources. For pikas this resource probably is the forage below the biting height of livestock, whereas livestock can reach forage on pastures far away by migration.

Keywords grazing, carrying capacity, small mammals, forage competition, Mongolia, live-stock, semi-arid

#### Introduction

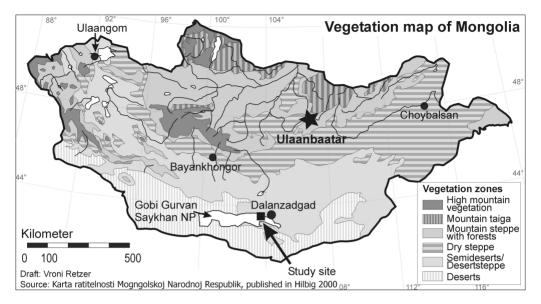
Grasslands are an important vegetation type worldwide; covering extended areas of more than  $16 \times 10^6 \text{ km}^2$ , hence accounting for 11% of the terrestrial surface of the earth (Sala, 2001). Semi-arid grasslands all over the world have been shaped by the grazing of large herbivores and soil-digging small mammals for millennia. The relative dryness of these steppes makes them unsuitable for reliable non-irrigated agriculture and therefore the traditional human land use is restricted to (nomadic) pastoralism.

Small mammals are widespread in the (semi-)arid steppe-ecosystems of the world. They are often regarded as pests for two main reasons: First, they are suspected to compete for forage with livestock (Shi et al., 2002; Zhang et al., 2003a,b). Secondly, herders are concerned about their burrows because the digging activity destroys the vegetation and may initiate a succession towards less palatable plants (Samjaa et al., 2000).

For Mongolia the preservation of the grazing capacity is of outmost importance as the by far the largest part of the country is used for the grazing of an approximately 30 Mio. heads of livestock. Their numbers increased after political transformation in the late 1980s and early 1990s (National Statistical Office of Mongolia, 2003) when the breakdown of industry, administration, and state farms forced many people to return to livestock keeping (Janzen & Bazargur, 2003; Müller, 1995).

For the administration of the Gobi Gurvan Saykhan National Park this increase was alarming as conservationists knew of the case of another small mammal, the Brandt's vole (*Microtus* 

<sup>&</sup>lt;sup>1</sup>Results of the Mongolian-German Biological Expedition since 1962, No. 247.



**Figure 1:** The location of the Gobi Gurvan Saykhan National Park in southern Mongolia. The study site lies approximately 80 km east of the Aymag capital Dalandzadgad.

*brandti*) in central Mongolia, which benefits from high grazing pressure and in turn initiates further range degradation. Populations of the Brandt's vole increase in numbers under conditions of intensive grazing by livestock, and voles are able to devastate large areas during mass population outbreaks and alter vegetation on the burrows (Zielinski, 1982; Peterson, 1984; Samjaa et al., 2000).

In the mountain ranges of the Gobi Gurvan Saykhan Mongolian Pika are the most abundant small mammals and if pikas could initiate a similar negative feedbacks there this would contradict the conservation goals of the park. Therefore, a research project was initiated to study the population ecology of the pikas (Nadrowski et al., 2002) and the forage competition between pikas and livestock (Retzer, 2004).

However, although the perception of small mammals as a pest is widely established, evidence actually proving forage competition is scarce. Often, assessments of forage competition are based on single indicators (such as overlap in resource use, see below) but are not investigated in detail. In general terms, forage competition between wild animals and livestock can be regarded as a special case of resource competition. Resource competition has been defined as "the negative effect [...] of acquisition of a particular resource by one species due to the use of this resource by another species" (Van der Wal et al., 1998; p. 228). Three conditions generally are widely regarded as prerequisites for forage competition (Begon et al., 1998; Van der Wal et al., 1998; Hulbert & Andersen, 2001):

- 1. overlap in habitat use,
- 2. share of the same forage resources, and
- 3. limited availability of the forage resource.

The potential forage competition of the Mongolian Pikas and livestock in the mountain steppe of the Gobi Gurvan Saykhan is studied with respect to these three assumptions.

## Study area

The Gobi Gurvan Saykhan National Park is situated in southern Mongolia and includes the southernmost outcrops of the Gobi Altay as well as vast areas of (semi-) desert (figure 1). Covering more than 21,700 square-kilometers it is among the largest national parks worldwide (Reading et al., 1999a). The park was established in 1993 in order to guarantee long-term sustainable land use, protection of rare wildlife, of (endemic) plant species, and of special landscape features, thus ensuring the undisturbed development of the ecosystems (WWF, 1993; Reading et al., 1999a,b).

The high altitudes belong to the core zone for protecting biotic diversity (Miehe, 1996; Miehe, 1998; Wesche et al., in review). They are also the habitat of rare and endangered species such as Argali (wild sheep), or Snow Leopard (Finch, 1996). Furthermore, the mountains receive more rainfall than the pediments and therefore sustain higher amounts of phytomass which serve as a forage reserve for the livestock of the herders living in the area (Retzer et al., in review). Pikas are abundant in the mountains, showing average densities of about 30 individuals/ha (Nadrowski et al., 2002; Retzer & Nadrowski, 2002).

The region is semi-arid with a mean annual precipitation of 131 mm in Dalandzadgad, interannual variation of precipitation is high (coefficient of variation = 36 %). Therefore, nonequilibrium dynamics prevail (Stumpp et al., in press). However, although annual precipitation totals are low, vegetation productivity is relatively high because 86 % of the annual precipitation is concentrated in the growing season (data Mongolian Meteorological Service, Retzer et al., in review). The vegetation changes with altitude and precipitation from desert steppes of the lower elevations to *Stipa gobica* steppes of the upper pediments, and to dry mountain steppes dominated by *Agropyron cristatum* and *Stipa krylovii* (Wesche et al., in review).

## Methods

#### The exclosure experiment

Phytomass production and intake of pikas and livestock was assessed by an exclosure experiment consisting of four different treatments: 1. access for livestock and pikas possible – pikas & livestock (no fence at all), 2. access only for livestock – only livestock (low, narrow wire fence), 3. access only for pikas – only pikas (high, wide wire fence) and 4. no grazing (combination of the two meshed wires). Each treatment was replicated four times (except for the first harvest in September/October 2001). Sampling started in October 2000 and took place every four to six weeks on  $1 \text{ m}^2$ -plots within every treatment and replicate.

A double-sampling technique (Bonham, 1989; Catchpole & Wheeler, 1992) was used to estimate standing crop. At each sampling date phytomass was harvested on half of the plots by clipping at minimum height and length (< 4 mm). Plots harvested once were not sampled again. Phytomass was dried on the stove to constant weight.

Standing crop on those plots that were not harvested was estimated based on two parameters, vegetation cover and height, as recommended for pasture and herbaceous vegetation (Catchpole & Wheeler, 1992). Vegetation height or volume worked well as predictor of standing crop in a number of other studies (Ward et al., 1998; Paton et al., 1999; Huennecke et al., 2001; Guevara et al., 2002).

Vegetation cover was estimated directly in percent and vegetation height was calculated as the average height of the three most abundant plant species or taxonomic groups Allium spp. (= mainly A. polyrrhizum and some A. prostratum), Stipa spp. (= S. krylovii and to a lesser extent S. gobica), and Agropyron cristatum which was measured with a ruler for each individuals of each species (or for all if less than twenty were present).

Due to substantial year-to-year differences between regression equations the data set had to be split and analyzed separately for the period before before 1st of May 2001 (equation 1) and afterwards (equation 2) (see also Johnson et al., 1988).

standing crop = 
$$2.41 + 0.0095 \cdot \text{cover} \cdot \text{height}$$
 (1)

standing crop = 
$$2.05 + 0.033 \cdot \text{cover} \cdot \text{height}$$
 (2)

Pikas managed to invade some plots of the treatment *no grazing* during the summer of 2001. Therefore, the values for the invaded plots were corrected by applying growth rates from undisturbed plots.

#### Calculation of productivity and intake

For the calculation of forage intake the paired-plot method was used (Bonham, 1989). Within each of the four exclosures first the average daily differences for each treatment (*no grazing, only livestock, only pikas, pikas*  $\mathcal{C}$  *livestock*) from one harvest date to the next were computed. These daily differences allow the comparison between sampling intervals of varying length. Missing values for one plot were replaced with the mean of the other replicates for this treatment. Then growth or intake was calculated separately for each replicate. Afterwards, the mean and standard deviation from the four replicates were computed.

Above ground net primary productivity (ANPP) was calculated by summing up all positive increments on treatment *no grazing* (Singh et al., 1975). This method proved to yield reliable estimates of ANPP for a semi-arid grassland steppe in Patagonia (Defosse & Bertiller, 1991) and also for a more humid grassland in Argentina (Pucheta et al., 1998).

Forage intake by herbivores was calculated by comparing standing crop on an area exposed to grazing (treatments *only livestock, only pikas*, and *pikas* & *livestock*) to standing crop on a reference treatment protected from grazing (*no grazing*, see Bonham, 1989). However, forage intake had to be calculated differently for phases of vegetation growth and non-growth conditions:

## Growth conditions

Intake during the growing season is determined by subtracting ANPP on the grazed area from ANPP within the exclosure (Pucheta et al., 1998). This assumes that plant growth was similar on all treatments and neglects possible trampling effects under grazing. Equation 3 shows the exemplary calculation for the intake by pikas. Intake is calculated analogously for livestock and both herbivore groups.

$$intake(pikas) = sc(n2) - sc(n1) + [sc(p1) - sc(p2)]$$
 (3)

sc(n1) is standing crop on treatment no grazing at date 1

sc(n2) is standing crop on treatment only pikas at date 2

sc(p1) is standing crop on treatment no grazing at date 1

sc(p2) is standing crop on treatment only pikas at date 2

#### Non-growth conditions

During non-growth conditions the process of plant decay had to be considered additionally. The same decay rate was assumed on both pairs studied (see also Wiegert & Evans, 1964 cited in Singh et al., 1975). Thus the percentage of decay observed on the treatment *no grazing* (term [sc(n1) - sc(n2)]/sc(n1) in equation 4) was proportionally subtracted from the standing crop on the other treatments:

$$intake(pikas) = (1 - \frac{sc(n1) - sc(n2)}{sc(n1)}) \cdot sc(p1) - sc(p2)$$
(4)

Again, forage intake is calculated analogously for livestock and both herbivores groups.

### Calculation of intake

Two options for calculating the intake are presented for comparison. Method A shows the values derived from adding up **all** increments while method B adds up only all **positive** increments of intake. Method A is generally recommended to minimize errors (see e.g. Biondini et al., 1991; Catchpole & Wheeler, 1992; Sala et al., 1988a). However, method B may be suitable when the errors made during positive intake seem to be much lower than those which cause the negative values. As this is the case within this study, where the highest impact of negative values was derived from the unreplicated first harvest, the results for both methods of calculation are given.

### Livestock densities

Livestock densities were estimated by direct observation from an elevated observation point using Russian binoculars ( $8 \ge 30$ ). Date and time of the observation were noted, and for every sighting the number and species of animals, and their distance and direction from the observation point was recorded. Numbers of goats and sheep were pooled as differentiation of the species in the mixed herds was impossible.

In winter during trips from the winter place towards the mountains additional data were collected. Distance and direction of the observed animals from a known point along the route was estimated in order to compute their position.

Livestock observation data were analyzed with the help of the geographic information system (GIS) ArcView 3.2 from ESRI. Animal densities were were converted into stocking units, the 'Mongolian Sheep Unit' (MSU) for better comparability. 1 MSU is equivalent to an intake of 365 kg of dry forage per day ( $\emptyset$ 1 kg/d). Therefore, 1 horse is equivalent to 7 MSU, 1 cattle or yak to 6 MSU, 1 camel to 5 MSU, 1 sheep to 1 MSU, and 1 goat to 0.9 MSU, respectively (Bedunah & Schmidt, 2000; Shurentuja et al., 2002).

#### Body condition scoring

Body condition scoring is a method to evaluate livestock's fitness by feeling the level of fat and muscling deposition over and around the vertebrate of the loin region (Thompson & Meyer, 1994). Each date, body conditions of ten adult female sheep and ten adult female goats from one herder near the research station were estimated in the period from November 2000 until September 2001. The scheme for sheep (Thompson & Meyer, 1994) was applied to both species as the author is not aware of a specific scheme for goats.

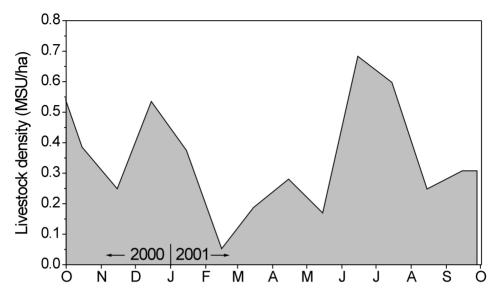
## Results

### Overlap of habitat use

Pikas are abundant in the steppes of the mountain ranges of the Gobi Gurvan Saykhan (Retzer & Nadrowski, 2002). Results of Karin Nadrowski (Nadrowski et al., 2002) show that in the Dund Saykhan pikas occur in all altitudes between 2100 m and the summit region at 2800 m. Pikas' density at the study site varied seasonally and interannually between 20–70 individuals/ha. Average density was 30 individuals/ha (Nadrowski, pers. comm.). The Mongolian Pikas are active in winter (Smith et al., 1990), and are therefore present all year round.

Livestock was also present in varying densities all year round (see figure 2). Livestock densities are controlled by forage availability and herders' migration strategies. In winter livestock densities at the study site were lower as herders took the small stock with them when they moved to their winter camps several kilometers to the south.

As the *Stipa-Allium*-steppes of the upper pediments were grazed by both herbivore groups at all seasons, habitat use of both groups overlapped.



**Figure 2:** Livestock density in the surroundings of the exclosure experiment from October 2000 until the end of October 2001. Densities are given in Mongolian Sheep Units per hectare (MSU/ha).

## Overlap of forage resource

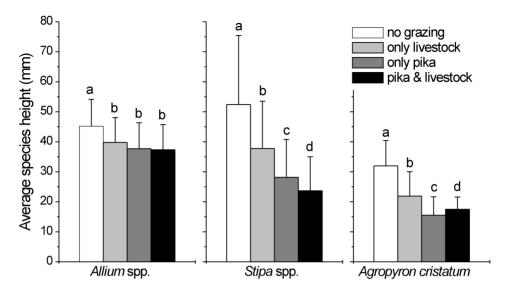
Figure 3 presents a comparison of the average height of *Allium* spp., *Stipa* spp., and *Agropyron* cristatum at the end of the growing season 2001 on the different grazing treatments. These three groups together accounted for almost 75% of the average available phytomass. Figure 3 shows that species height has been significantly reduced on all grazed variants. The grazing impact on *Stipa* spp., and *Agropyron cristatum* was more serious than that on *Allium* spp. Therefore, it can be concluded that those two were preferred over *Allium* spp. by both herbivore groups. However, although grazing intensity varies all three species are grazed.

Therefore, it can be concluded that both herbivore groups use the same forage resources at the study site.

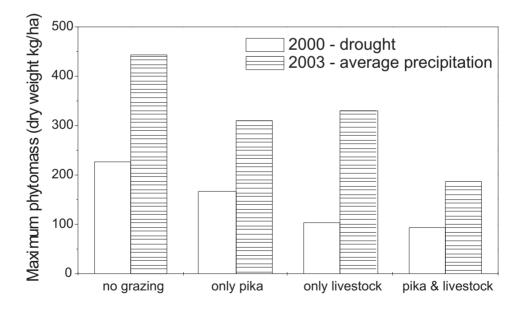
## Scarcity of forage resource

During the study period southern Mongolia experienced a severe drought. The herders in the vicinity of the research camp regarded conditions in the summer of 2001 as an extremely heavy drought (own unpublished interviews). Precipitation at the research camp in July and August of 2001 was only 16% of the amount received in 2000 and 19% of that received in 2003. For both of the years 2000 and 2003 average precipitation levels were recorded (Retzer, 2004; data from Nadrowski, K., Wesche, K., Retzer, V.).

This lack of precipitation was reflected in the phytomass production. Figure 4 compares the maximum amount of standing crop recorded at the four different exclosure treatments in 2001 with those recorded in 2003. Maximum standing crop in the year of drought was reduced to a mere 30–50 % of that in years with average precipitation. This also had practical consequences for livestock in the area. Body condition scores should be at maximum just at the end of summer and decrease continuously during winter as the stored fat is burned. In 2001, however, body condition scores of sheep and goat are worse at the end of September 2001 than they were in December 2000 (see figure 5). This indicates that the animals failed to accumulate as much fat reservoirs as in the 'normal' year 2000 because in 2001 forage resources were less than sufficient



**Figure 3:** Average height of the most important species/groups *Allium* spp., *Stipa* spp., and *Agropyron cristatum* at the end of the growing season 2001 (September 2001). Significant differences between the four grazing treatments for each species are marked by different letters (single-factor ANOVA, post-hoc Bonferroni corrected, p < 0.05).



**Figure 4:** Comparison of the maximum amount of phytomass measured on the different treatments during a dry year (2001) and an slightly above average year (2003). During the drought in the summer of 2001 phytomass is reduced to 30–50 % of the level of a year with average precipitation. Phytomass data for 2003 courtesy Wesche, K. and Pietsch, M., unpublished.

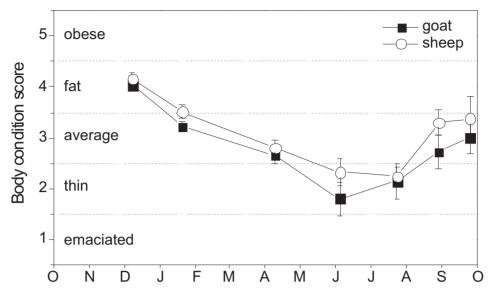


Figure 5: Average body condition score of each ten female sheep and goat of one herder living in the vicinity of the study site.

for livestock. Population parameters of the pikas show that pikas were negatively affected by the scarcity of forage resources, as well (Nadrowski, pers. comm.).

Therefore, all three prerequisites mentioned above were met, and forage competition between pikas and livestock can be assumed for the year 2001.

### Forage intake by pikas and livestock, respectively

Table 1 shows the intake by both groups expressed in absolute numbers, and expressed as percentage of the available phytomass. For comparison, two ways of calculating the intake are presented. method A and B (see methods section for further explanation).

In the growing season 2001 net primary productivity, as measured on treatment *no grazing*, was 184 kg/ha. Additionally, 43 kg/ha remained from the previous growing season. Therefore the available phytomass (column 'available' in table 1) was 227 kg/ha. Of this, after calculation method A, 107 kg/ha were consumed by livestock on treatment *only livestock*, 148 kg/ha by pikas on treatment *only pikas*, and 150 kg/ha on treatment *pikas* & *livestock*. In September 2000 51 kg/ha of potentially available phytomass were left additionally, so the total available phytomass for the period 09/2000–09/2001 summed up to 279 kg/ha. From these data the proportion of consumed phytomass could be calculated: During the growing season of 2001 66–76 % are consumed by both herbivore groups (on treatment *pikas* & *livestock*)– depending on the method of calculation. For the whole investigation period the range of this percentage was similar: 57–76 %.

During the growing season 2001 pikas dominated the intake on treatment pikas & livestock. The forage intake on the latter treatment was only slightly higher than on treatment only pikas. Possibly pikas consumed the maximum amount accessible to them on both treatments. The fact that the disappearance on treatment pikas & livestock was still slightly higher than on treatment only pikas may be attributed to the additional trampling impact of livestock on this treatment.

Growing season intake on treatment only pikas was highly significantly correlated with that

**Table 1:** Absolute intake of livestock, pikas, and livestock & pikas, respectively, in the growing season 2001 (above, 04/2001-09/2001) and during the whole investigation period (below, 09/2000-09/2001) in kg/ha and expressed as a percentage of the available phytomass. A and B indicate two different methods of calculation. A: summing **all** increments of intake, and B: summing **all positive** increments. See text for further explanation.

growing season 2001					
04-09/2001	livestock	pikas	$pikas \ {\ensuremath{\mathcal E}}\ livestock$	available	
A (kg/ha)	107	148	150	227	
A (%)	0.47	0.65	0.66		
B (kg/ha)	143	167	172	227	
B (%)	0.63	0.73	0.76		
one year					
09/2000-09/2001	livestock	pikas	pikas & livestock	available	
A (kg/ha)	105	151	158	279	
A (%)	0.38	0.54	0.57		
B (kg/ha)	151	226	211	279	
B (%)	0.54	0.81	0.76		

on treatment *pikas & livestock* (Pearson's  $r^2 = 0.99$ , p < 0.001), while the correlation between intake on treatments *pikas & livestock* and *only livestock* was not significant (Pearson's  $r^2 = 0.51$ , p = 0.18).

Considering all methods, livestock consumed about half of the available phytomass (38-63%), while pikas consumed considerably more: 54-81%. Furthermore, the percentage of intake by both groups was similar to that by pikas alone: 57-76%.

Whatever the exact numbers are, the two methods provide at least a minimum and maximum estimate of the intake. The following patterns can be detected with either method:

- 1. Pikas consume a higher amount of the vegetation than livestock does. This holds true for both methods of calculation and both periods of investigation.
- 2. The intake of pikas alone was always more similar to that of *pikas* & *livestock* than to that of livestock alone. This, too, holds true for both methods of calculation and both periods of investigation.

## Discussion

In field experiments with focus on forage competition, intake is rarely measured directly. Most studies are based on single indirect indicators such as overlap of habitat or forage species (e.g. Dawson & Ellis, 1996; Van der Wal et al., 1998). Exclosure experiments have frequently been used to quantify the grazing impact by livestock on phytomass (Brathen & Oksanen, 2001; Meurer, 1998). But only few investigations use exclosure experiments as a method to evaluate competition between two different groups of herbivores, as was done in this study.

#### Comparison of large herbivore densities and intake

McNaughton et al. (1996) suggest to compare values for animal intake with estimates of "how much they *should* have consumed" (p. 974, emphasis added) in order to trace errors made during the calculation. Figure 6 shows a comparison of livestock densities (see figure 2) with livestock

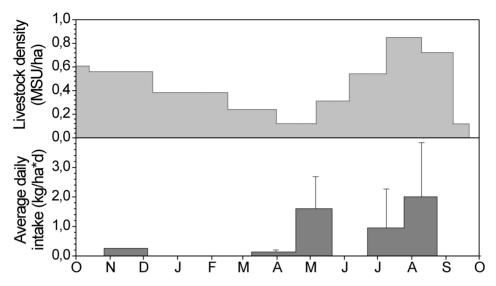


Figure 6: Comparison of livestock densities (in MSU/ha) with calculated intake by livestock (kg/ha·d) during the investigation period.

intake (see table 1) during the investigation period. Livestock density is given as MSU/ha, which is equivalent to the unit in which intake is measured: kg/ha·d, as 1 MSU is defined as an average daily intake of 1 kg dry matter.

Both data sets allow to sum up the intake for the whole investigation period (table 2). However, both figures should be compared for the period of a whole year, because one MSU consumes 1 kg/d on average with a high seasonal variability.

For the budget of the whole year the values for the intake derived from animal observations and calculated from the exclosure experiment are relatively similar. Both estimate a intake of approximately 120–130 kg/ha·a. The fact that estimates derived from such widely different experiments yield approximately similar levels of forage intake indicates that both methods worked satisfactorily.

## Coexistence versus competitive exclusion?

In its simplest form ecological theory predicts that the more powerful competitor excludes the less powerful one from the resource in question (Begon et al., 1998). Nevertheless, pikas and livestock coexist in the mountain-steppes of the Gobi Gurvan Saykhan. Not even a severe drought such as that encountered in the summer of 2001 leads to the competitive exclusion of one of the species. Therefore, it has to be asked, which mechanisms make this coexistence possible. Models have shown that competing species can coexist when each species has free access to another resource not in competition (Belovsky, 1984; Schoener, 1974; both cited in Van der

**Table 2:** Comparison of the intake by large herbivores (kg/ha·year) derived from animal observations and the exclosure experiment, respectively. Data for the exclosure experiment are shown for two methods of calculation A & B (see above).

$\mathbf{experiment} \rightarrow$	animal observation	exclosure
intake of large herbivores (kg/ha·year)	120	105 (A) - 151 (B)

Wal et al., 1998). This mechanism may also explain the coexistence of pikas and livestock: pikas have a higher competitive power in the *Stipa-Allium*-steppe, while livestock can access forage resources not accessible to pikas by moving to different grazing grounds. In this scenario both groups have access to a mutually exclusive forage resource and therefore coexistence at the study site is possible.

This idea is supported by the empirical evidence presented here: Pikas seem to be the herbivores with the higher competitive power, for three reasons:

- 1. They have the advantage of being and grazing on the spot virtually all the time.
- 2. Their small size and mouth anatomy allows them to bite certain plants down to lower heights than livestock can (Miehe & Miehe, 2000; see figure 3). This is in accordance with simulation experiments showing that among grazing ruminants those "of smaller body size are competitively superior to larger ones due to allometric relationships of bite size and metabolic requirements to body size" (Clutton-Brock & Harvey, 1983, cited in Hulbert & Andersen, 2001 p. 499).
- 3. Under conditions of limited forage availability, pikas consume higher amounts of the forage in competition (table 1).

This interpretation is supported by findings from a recent modelling approach that shows that smaller grazers are generally competitively superior over larger ones (Farnsworth et al., 2002). The fact that pikas have access to forage which is not subject to competition with livestock allows them to stay on the site and survive periods of drought.

The most important herding strategy for livestock in extremely variable non-equilibrium rangelands is opportunistic migration in relation to actual forage availability (see e.g. Behnke et al., 1993; Westoby et al., 1989; Sullivan & Rohde, 2002). This is the forage resource which is exclusively accessible to livestock due to their superior mobility. During droughts livestock is moved to better grazing grounds thus escaping local competition with pikas (for a model of this see Retzer & Reudenbach, in review).

## Conclusion

Mongolian Pikas and livestock consume the same forage plants within the same habitat and compete for forage at least during times of forage scarcity. Pikas are competitively superior and consume more phytomass than livestock does. Nevertheless, pikas and livestock can coexist in the mountain steppes of the Gobi Gurvan Saykhan because both groups have access to a mutually exclusive forage resource. Livestock migrates to regions with higher rainfall and productivity, while pikas use the vegetation on the site more efficiently. In a year of drought both strategies may not be enough to sustain the populations, but the mechanism of differential resource use prevents the competitive exclusion of one of the herbivores.

Although forage competition between pikas and livestock has been shown, pikas cannot be necessarily regarded as a pest. On their burrows they positively influence forage productivity and seasonal availability also for livestock (Nadrowski et al., 2002; Retzer, 2004). Thus, the amount of forage consumed by pikas cannot simply be converted into higher livestock densities in the absence of pikas.

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