Modelling the carrying capacity and coexistence of pika and livestock in the mountain steppe of the South Gobi, Mongolia

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Abstract

Forage competition between small mammals and livestock is of crucial importance in most semi-arid and arid regions of the world. In order to improve the forage availability for livestock small mammals have been the target of eradication worldwide. However, in most of these regions the ecosystems are governed by non-equilibrium processes which have overwhelming influence on livestock densities. Due to these ecosystems' highly variable natural environment, field observations are usually insufficient to describe the whole system as they usually are too short to cover all significant states. Thus we used field information on processes and additional literature information to drive a dynamic model simulating forage competition between the Mongolian pika (*Ochotona pallasi*) and livestock in the Mongolian South Gobi.

The regulatory mechanisms of pika's territoriality and herders' migration strategy as implemented in the model proved to be sufficient to keep the densities of both herbivore groups within the observed and denoted limits. Both groups can coexist because each has exclusive access to a forage resource unavailable to the other group: pika have the ability to bite down the vegetation deeper than livestock can while the herders drive livestock to better pasture grounds out of reach of the pika when forage is scarce. Nevertheless, both groups react to the frequent periods of forage scarcity and thus indirectly interact via forage competition. The model shows that the large increase in livestock numbers after the Mongolian socio-economic transformation cannot be singularly explained by favourable weather conditions during that period. Only a change in herding strategies with higher livestock densities can explain the observed increase in numbers. However, the larger numbers were short-lived as the risky strategy succumbed to adverse weather conditions in the late 1990s and livestock numbers crashed in reality as well as in the model. This indicates that in the non-equilibrium system livestock numbers are regularly forced well below the average carrying capacity. Thus, livestock densities are largely controlled by the variability of the abiotic conditions – namely precipitation – and previous levels of livestock densities cannot be increased in the long term as herding strategies are already optimised.
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1. Introduction

Competition and predator–prey dynamics have long been regarded as major factors driving ecosystem processes and population dynamics (MacArthur, 1972; Stephens and Krebs, 1986). Both aspects, however, are difficult to be studied in the field, competition because it cannot be measured directly and predator–prey dynamics because a long time series of data is needed especially for larger animals.

Due to the high inter-annual variability forage competition is even more difficult to assess in non-equilibrium ecosystems, as an extremely long time-series of field data is needed and such data are generally lacking. Process-oriented modelling is a well-established approach to overcome this problem, and models focussing on the comprehension of ecosystem processes requiring only a few parameters can help to promote the understanding of the effects of competition (Bossel, 1994; Gotelli, 2001). Existing models in the field of range ecology dealing with processes are focussing either on detailed studies of the grazing process (Cohen et al., 1999; Hutchings and Gordon, 2001), grazing impact on vegetation (Weber et al., 1998; Jeltsch et al., 2001), a general description of the predator–prey dynamics (Neubert et al., 2004; Tschirhart, 2004), optimal harvesting (Hearne et al., 1996; Virtala, 1996; Georgiadis et al., 2003; Stigter and van Langevelde, 2004; Jensen, 2005), or with evaluating the ecological sustainability of management alternatives (Cooper and Huffaker, 1997; Janssen et al., 2000; Diaz-Solis et al., 2003). Wu et al. (1996) suggest a general model for grazing systems in semi-arid areas using probabilistic and fuzz parameters, but do not include forage competition between the herbivores. Regarding forage competition between livestock and wild herbivores existing models focus on the competition of livestock with large wild herbivores (van Kooten et al., 1997; O'Connor and Kiker, 2004), but although long-term livestock carrying capacity in semi-arid regions under high inter-annual precipitation variability and the competition between small mammals and livestock are of global interest, the authors are not aware of any other model dealing with both aspects. Therefore, here we present the results of our model for assessing pika's status as a 'rodent pest' and derive implications on the long-term carrying capacity of the dry mountain steppe in southern Mongolia.

1.1. The case study in southern Mongolia

The biomass production of the Mongolian steppes is the basis for the nutrition of about 26.1 million heads of livestock (2001), which in turn are the livelihood basis of the country's rural population (National Statistical Office of Mongolia, 2002). The predominant management strategy is pastoral nomadism; it accounts for about 30% of the GDP in Mongolia (Worldbank, 2002). The abiotic conditions of livestock herding are extreme, with winter temperatures dropping to $-40\,°C$, a short vegetation period and high rainfall variability (Barthel, 1983). Any deterioration of the forage availability results in higher mortality and thus negatively affects the 185,546 herders' households (2001), which directly depend on their animals (National Statistical Office of Mongolia, 2002).

Therefore the competition for forage with wild herbivores is a point of concern. While many wild large herbivore species have been severely reduced in numbers in the past (Reading et al., 1999a, 1999b; Mix, 2000) the focus still is on small mammals. The interactions between herbivores of different sizes are manifold. Extensive literature exists on the positive feedbacks of prairie dogs (*Cynomys* spp.) and their colonies on the forage availability of bison in the North-American steppe (prairie) (Coppock et al., 1983; Krueger, 1986; Kotliar et al., 1999; Bangert and Slobodchikoff, 2000; Fahnestock and Detling, 2002). But in the steppes of Mongolia and Inner Mongolia another small mammal, the Brandt's vole (*Microtus brandti*) is regarded as a pest. It could be shown that Brandt's voles initiate a successional cycle on their burrows towards plants which are less favourable as livestock forage (Samjaa et al., 2000). The impact of Brandt's vole is especially disastrous during their population outbreaks and it seems to be facilitated by high densities of livestock grazing (Shi et al., 2002; Zhang et al., 2003a, 2003b). Similar processes have been reported from the steppes of Eastern Mongolia for the Daurican pika (*Ochotona daurica*) (Shi et al., 2002; Zhang et al., 2003a, 2003b). Negative effects on livestock have resulted in eradication programmes for both small mammals in Mongolia and in China (Shi et al., 2002; Zhang et al., 2003a).

Mongolia has been undergoing a fast and relatively smooth transformation from a Soviet satellite state to a free market economy after a peaceful 'revolution' in

1991 (Fish, 2001). The collapse of the socialist system and the associated breakdown of the economy led to a sharp drop in urban employment. Many Mongolians balanced the resulting unemployment by turning back to the roots: they started to survive as pastoralists and the so called "new nomads" were born (Muller, 1995; Janzen and Bazargur, 1999; Janzen, 2000). This lead to an extreme increase in livestock numbers until 1999 and an equally sharp decline until 2002 following suboptimal weather conditions. The impact of this new era in pastoral nomadism in Mongolia on the ecosystems is still not well established, though concern has arisen that it may facilitate pasture degradation (Batkhishig and Lehmkuhl, 2003). In the "Gobi Gurvan Saikhan" national park the example of the Brandt's vole in Northern Mongolia in combination with the increase of livestock after the transformation gave rise to concern that a similar vicious cycle would be initiated in the mountain steppes of the South Gobi. There, the Mongolian pika (*Ochotona pallasi*) is the dominant and most prominent small mammal (Nadrowski et al., 2002). Not much is known about its biology nor about its interactions with its physical environment and competition with other herbivores (Smith et al., 1990; Schneider, 1988). Therefore, a research project was set up to investigate their biology and potential for competition with livestock to assess their function within the ecosystem. Data from 1.5 years of fieldwork within this project were used to set up and drive the model presented.

The following four questions which arose from the fieldwork were the guidelines to define and focus the aims of the model:

1. Is long-term coexistence of pika and livestock possible, as fieldwork suggests?
2. How strong is the impact of competition on either side?
3. Are the high numbers of livestock after the transformation the result of a series of 'good' years of relatively favourable weather conditions, or did herding strategies change?
4. What can we learn about the long-term carrying capacity of the system?

The model therefore should be capable of projecting the dynamics and the interaction of the densities of small wild herbivores (pika) and large domestic herbivores (livestock) in a qualitatively and quantitatively valid fashion.

2. Materials and methods

2.1. Study area

The field data was gathered in the mountain steppe of the Gobi Gurvan Saikhan range in Southern Mongolia from June 2000 to September 2001, and again in June/July 2002. The study site was situated on the southern face of the Dund Sayhan Mountain (Middle Beauty) at about 2350 m at the upper end of the pediment. The area is semi-arid; rainfall is concentrated in the summer months and is very variable inter-annually as well as spatially (Barthel, 1983). The summer of 2000 was about average, while the consecutive 2 years were very dry.

The whole area is used as pasture by nomadic herders. As common in Mongolia, the large livestock species camels (*Camelus bactrianus*), horses (*Equus caballus*), cattle (*Bos taurus*) and yak (*Bos grunniens*) roam freely, while sheep (*Ovis aries*) and goat (*Capra hircus*) are herded and return to the ger (mobile home) every night. Pika are abundant in this altitude and show densities of 25–35 animals per hectare (Nadrowski et al., 2002). There are also other small mammalian herbivores including the Mongolian gerbil (*Meriones unguiculatus*) or Grey hamster (*Cricetulus migratorius*) and large wild herbivores such as Black-tailed and Mongolian gazelles (*Gazella subgutturosa* and *Procapra gutturosa*), Siberian ibex (*Capra sibirica*) and Argali wild sheep (*Ovis ammon*) in the area. They are sub-summarised under the terms 'pika' for small herbivores and 'livestock' for large herbivores respectively because those two groups account for more than 95% of the biomass in each herbivore group (Nadrowski et al., 2002; Retzer, 2004).

2.2. Field methods

The data on pika were gathered using a regular live-trapping scheme with Sherman live-traps and observation of the animals on 1 ha. Trapping data were used for the calculation of pika numbers and their reproductive potential. The observational data on pika behaviour, especially on their territoriality were used to model pika's mortality rate (called 'pika's territorially death' in the model description). Data on burrow densities and burrow areas were recorded by mapping and measuring out more than 40 burrows. Burrow creation and decay

was followed on one marked burrow over two consecutive years. Livestock densities were observed from an elevated observation point.

Production data of vegetation were assessed by double-sampling of an exclosure experiment. It consisted of four different variants: (1) access for livestock and pika possible (no fence at all), (2) access only for livestock (low, narrow wire fence), (3) access only for pika (high, wide wire fence) and (4) no grazing (combination of the two fence types). Each variant was replicated four times. Data collection took place in roughly monthly intervals. This experiment was used to calculate pika requirements, pika's foraging advantage, rain use efficiency of the vegetation, and the amount of biomass which could be harvested by the scientist, but was not accessible to the animals (∼30 kg/ha). Similar exclosure experiments on pika burrows were used to assess the influence of the pika's digging activity on vegetation productivity (Wesche et al., 2003; Retzer, 2004).

Basically all data on pika, pika burrows, and pika behaviour were collected by Nadrowski (Wesche et al., 2003; Nadrowski et al., 2002), while data on vegetation productivity, food competition, and livestock densities came from Retzer (2004). Additionally, information was gathered from interviews with local herders and by participatory observation. For more details regarding the investigation methods see Retzer (2004) and Nadrowski et al. (2002). Further information was acquired from the literature. An array of statistical yearbooks on Mongolian agriculture provided especially useful information on the development of the livestock sector (National Statistical Office of Mongolia, 1996, 1998, 2000, 2001, 2002, 2003). The precipitation data for Dalandzadgad from 1937 to 2002 were obtained from the Meteorological Service of Mongolia. The data up to 1999 are compiled in Bergius (2002); those for 2000–2002 were directly obtained from the Meteorological Office in Dalandzadgad. Long-term precipitation data reconstructed from tree ring investigations in northern Mongolia for the period 1651–1995 (Pederson et al., 2001a,b) were used for validation and to check the long-term stability of the system.

3. Model description

Qualitatively the validity of the model is assumed, when a stable system can be reproduced over a period of 50 years. Stability in this context does not mean constant population numbers but that the population numbers vary within a reasonable (observed) range and that none of the populations becomes extinct. Quantitative validity is given when the population densities and phytomass production under drought conditions are close to those observed during the field campaign.

Time steps of 1 year were chosen as the model's temporal resolution. This means that all intra-annual (seasonal) processes have to be balanced before being included into the model. The spatial level was standardised to 1 ha, ignoring any spatial gradients. Furthermore, for simplicity all simulated stocking rates of livestock are expressed in terms of livestock units, the Mongolian Sheep Unit (MSU). One MSU roughly represents the grazing capacity of one Mongolian sheep, 365 kg dry matter per year (Shurentuja et al., 2002). The model simulates the functional response of competition between two groups of herbivores. The central variables steering the system dynamics are the production of vegetation biomass triggered by precipitation and the intake by livestock and pika. The main regulation of animal densities and the prerequisite for coexistence of both herbivore groups are two different foraging strategies. Through their smaller size pika can exploit a higher percentage of the available vegetation than livestock on the site (Farnsworth et al., 2002; Retzer, 2004), while livestock can avoid severe forage shortages by movement to better pastures (Sheehy, 1993).

All variables used to drive the model are listed in the appendices. Appendix A lists the initial values derived from field data, the runtime variables, and the constants from literature and field observations, while Appendix B lists the Gauss normally distributed filter functions deduced from the statistical livestock data.

3.1. Production of vegetation biomass

Ecosystems which are primarily driven by low amounts of precipitation of high variability are supposed to behave in a non-equilibrium manner (Behnke et al., 1993; Sullivan, 1996). Under these conditions the influence of the variable rainfall pattern on plant production is much more important than density-dependent feedback mechanisms from herbivores. Fernandez-Gimenez and Allen-Diaz (1999) showed in a recent case study in neighbouring Bayankhon-

gor Aymag that the desert-steppe under investigation behaved in a non-equilibrium way, while the steppe reacts in an in an intermediate way and mountain-steppe in a more equilibrial way. In terms of annual precipitation and its coefficient of variation our study site lies somewhere between the desert-steppe and steppe of Fernandez-Gimenez and Allen-Diaz. Additionally no gradient of grazing impact could be found in the investigation area except from the trampling impact at the immediate surroundings of wells (Stumpp et al., 2005). Therefore, non-equilibrium conditions were assumed for the model. This implies that vegetation growth is triggered by precipitation only, and that density effects of livestock on vegetation are neglected. Thus, vegetation growth is directly triggered by the annual precipitation dynamics.

The experimentally derived rain use efficiency (*RUE*) of the vegetation describes the production of dry vegetation per mm of precipitation (Le Houerou, 1984) and can be used to convert annual precipitation sums into productivity for estimating potential livestock production (Guevara et al., 1996). However, as pika burrows are more fertile than the steppe matrix, the area has to be split into two zones of productivity: burrow area (B_A as derived from the field experiments) and steppe matrix area (S_A). Pika burrows are by the factor bV more productive than the steppe matrix. Therefore overall rain use efficiency (*RUE*) is calculated from the rain use efficiency derived from the field experiments for the steppe matrix (*rue S*) by:

$$RUE = rue\,S \times (S_A + B_A \times bV)$$

The annual precipitation data from Dalandzadgad are continuously available from 1937. The amount of precipitation was comparable to the precipitation recorded at the camp during the investigation and is therefore used to drive the model (*R*). However, *RUE* cannot be used directly as an estimator for phytomass production as a constant amount of vegetation biomass per hectare can be harvested by the human researcher but cannot be consumed by any of the herbivores (*v*). This is due to the harvest method, as all phytomass which could be reached was collected. However, it turned out that from this an amount of approximately 30 kg/ha was not accessible to neither livestock nor small mammals as this phytomass remained on the plots during winter regardless of grazing intensity (Retzer, 2004). Therefore, this amount of phytomass has to be subtracted

from the produced phytomass in order to get the net vegetation biomass *V*:

$$V = RUE \times R - v$$

3.2. Competition

The core idea of the implementation of competition is based on a comparison of the forage demand of pika and livestock with the net available vegetation biomass. Using the ratio of forage demand of pika (F_P) and livestock (F_L) and net vegetation biomass (*V*), the potential consumption ratio (*PCR*) is standardised according to:

$$PCR = \frac{F_P + F_L - V}{V}$$

to derive a dimensionless unit. The mean *PCR* ($\overline{PCR}$) of the actual and the previous year is then:

$$\overline{PCR} = \frac{PCR_t + PCR_{t-1}}{2}$$

PCR is used as a binary decision criterion to determine whether or not both populations have access to a sufficient amount of forage to satisfy their needs. Competition occurs if *PCR* is greater than zero. Consequently animals will starve if other adaptation opportunities such as hay stocking or emigration prove inefficient to make up for the missing forage. Due to a coarse classification of the observed and statistically derived numbers of herbivores the following conditions were implemented.

The starvation process of the pika population is initiated if:

$$PCR > 0$$

and that of livestock if:

$$\overline{PCR} > 0$$

In general, these conditions can be interpreted as a simple implementation of the metabolism of both the herbivore groups: while livestock can partially rely on stored body fat from last year, and therefore can cope with some adverse conditions, pika do not store body fat and need constant access to forage. The impacts of competition on the herbivore populations, such as emigration, starvation, etc. are discussed in the separate sections of livestock density dynamics and pika dynamics.

3.3. Livestock density dynamics

The density of domestic herbivores for centuries has been largely controlled by the opportunistic management decisions of the herders. They try to optimise (=maximise numbers while minimising losses) their livestock numbers by adapting their migration strategies to the forage availability (Dean and Macdonald, 1994; Ward et al., 1998; Illius et al., 1998). This assumes that livestock are slaughtered before they reach maximum age; therefore, death from old age can be ignored. Livestock losses due to diseases and predator attacks are relatively rare and poorly documented. Furthermore, such losses often are interrelated with other causes such as drought. Thus, such losses have not been modelled separately but sub-summarised under other causes of livestock deaths. Water as a limiting factor can be neglected because water points and wells are frequent around the mountains of the Gobi Gurvan Sayhan (Schmidt, 2000). Animal diseases do not seem to be a major problem at the moment and are explicitly not included into the model. The processes regulating the livestock population thus are reproduction (Abel and Blaikie, 1990; Scoones, 1993; Georgiadis et al., 2003), slaughter, and starvation. Regarding the migration strategy herders generally have the intention to stay where they have traditional pasture rights. As a result they immigrate with a higher priority than they emigrate.

Therefore, the fundamental processes for livestock dynamics are reproduction, emigration (leaving the model hectare in search for better pasture elsewhere), immigration (returning to the model hectare), starvation and slaughtering. Because the model has a timely resolution of 1 year, the following basic assumption regarding the timing of the processes are made:

1. The first response to lack of forage is *emigration*.
2. *Starvation* takes place if insufficient forage availability cannot be balanced any longer by energy stored as body fat.
3. *Slaughtering* affects all livestock, emigrating or not, except those that died of starvation.
4. *Immigration* is possible only if the estimation of forage availability indicates a surplus when compared to the forage needs of the livestock already in place.

3.3.1. Emigration

Whenever forage is not sufficient ($PCR > 0$) herders have to decide whether or not they migrate their livestock towards another pasture. The emigration decision is based on the standardised PCR as a direct reaction to the forage competition of any given year:

- If $-1 < PCR < 0$ forage is sufficient and there is no need to emigrate.
- If $0 \leq PCR < 1$ forage supply is insufficient and herders start emigrating.

To meet the assumed trend to minimise emigration activities, an empirically derived linear relationship is implemented for the factor of livestock emigration mL which intends to minimise emigration activities. The upper threshold should be smaller than 1.0 and therefore is set to 0.9. The factor of herders' emigration wish (mH) is then derived from:

$$mH = a(mH) + PCR \times s(mH)$$

The forage deficit (F_d) is calculated from the actual demands of pika and livestock populations according to:

$$F_d = V - (F_P + F_L)$$

To simulate the fact that herders do not have exact knowledge of future precipitation and phytomass production, the amount of total forage deficit is multiplied with a normally distributed Gauss filter function (see Appendix B, gF_d) to add some statistical noise. Furthermore, only non-slaughtered livestock on the 1 ha plot can emigrate. Therefore the number of emigrating livestock is at most $L - L_{st}$. The number of emigrating livestock is then finally derived from:

$$L_m = \frac{gF_d}{fL} \times mH \quad \text{if}$$

$$gF_d > 0 \wedge mH > 0 \wedge L_m < L - L_{sl}$$

3.3.2. Immigration

The model variables describing emigration and immigration have to be based on different premises to avoid an unreal auto-correlation of herders' decisions. Furthermore, the decision for immigration is more speculative, as the decision to immigrate has to be made early in the year without exact knowledge about precipitation and vegetation productivity. Therefore, at the 'beginning' of each year potentially available phy-

tomass (V_e) is estimated using a normalised running mean of precipitation for the last 3 years (R_3). Subsequently the intensity of the herders' wish to immigrate is derived from a linear relationship depending on the normalised rainfall by comparing this estimated forage availability to the forage demand of the actual stocking rate (=potential livestock deficit). If there is more available phytomass, additional livestock immigrates. The number of immigrating livestock (L_r) is determined by multiplying this herders' immigration wish (rH) with the deficit of livestock with respect to the estimated available biomass (V_e) and livestock already in the area (L).

Vegetation biomass of the actual year is estimated according to:

$$V_e = R_3 \times RUE - F_P - v$$

And the intensity of herders' immigration wish according to:

$$rH = a(Hr) + \frac{R_3 - R}{r} \times s(Hr)$$

The number of immigrating livestock is subsequently calculated as:

$$L_r = \frac{V_e - F_L}{fL} \times rH \quad \text{if } rH > 0$$

This implementation is based on the assumption that external herders only want to immigrate if there is sufficient forage for both the livestock already on the plot and the immigrating livestock. The numbers of immigrating livestock are simply added to the numbers of livestock already in the area. This implementation results in a decoupling of the emigration and immigration controls avoids artificial feedback between both the processes.

It has to be stressed that although the parameters currently used to control the emigration and immigration dynamics ($a(Hm)$, $s(Hm)$, $a(Hr)$, and $s(Hr)$) are fixed empirically, they are not arbitrary. The criterion was that in the long run the migration strategy has to maintain a balance between emigration and immigration. Thus several combinations of values were tested and the one resulting in the smallest influx of livestock into the model hectare was finally chosen. A small influx could be tolerated because the Mongolian statistical data indicate that the South Gobi has a negative livestock balance as reproduction numbers are lower

than would be necessary to sustain livestock numbers. Therefore, it can be assumed that more livestock enter the area than leave it.

3.3.3. Reproduction

The main process resulting in an increase of livestock numbers is the reproduction of the animals. As no significant correlation with high explanatory value between reproduction and several precipitation parameters could be found, it is implemented randomly using the Mongolian statistics of livestock reproduction rates since 1939. Each time step a random Gauss normally distributed reproduction rate (rpL) based on the statistical moments derived from these figures (Appendix B presents the coefficients) is applied to the actual total numbers of livestock:

$$L_{rp} = rpL \times (L + L_r)$$

3.3.4. Slaughtering

The slaughter rate (slL) is implemented analogously to the reproduction rate. A random Gauss normally distributed slaughter rate (Appendix B) with the parameters derived from the Mongolian statistics on agriculture is applied:

$$L_{sl} = slL \times L$$

3.3.5. Starvation

Livestock die of starvation (L_{st}) – if they did not emigrate or were slaughtered – if the mean *PCR* of two subsequent years $\overline{PCR}$ is positive. This conditions indicate that livestock could not fill up fat deposits for two subsequent year s and therefore is prone to die from starvation:

$$L_{st} = stL \times L \quad \text{if } \overline{PCR} > 0 \wedge L - (L_m + L_{sl}) > 0$$

3.3.6. Livestock numbers

Summarising all the previous equations the integral number of livestock at each time step is derived from:

$$\Delta L = L + L_r + L_{rp} - L_{sl} - L_{st} - L_m$$

3.4. Pika population dynamics

The dynamical patterns of the population of pika were implemented according to the following field observations:

1. Each pika needs a burrow for survival. The burrow protects it from cold and predators and provides sleeping, nesting, and storage chambers for hay. As each pika generally inhabits its own burrow and defends a territory, the number of available burrows limits the number of overwintering adult pika. Therefore, the maximum number of pika is a functional relation of the number of available burrows (∼territories).
2. Burrow creation and decay is a very slow process: within 1 year changes are barely visible.
3. Under average conditions pika always reproduce a sufficient number of juveniles to 'refill' any empty burrows.
4. Pika have a competitive advantage in obtaining and storing forage in comparison to livestock.

Pika's territorial behaviour allows for an elegant simplification of the implementation of pika's death. As the territories are occupied by the most vital individuals, those pika without a burrow are much more likely to fall prey to a predator or die of diseases. Furthermore, any time one of the 'burrow owners' dies of any of these causes it will be replaced by the fittest animal without a territory. This allows to summarise all causes for death – except starvation – under a single parameter 'pika territoriality death'. As the burrows are remarkably stable we also regard the modelled pika population as stable in the long term and assume that any extraordinary events killing a large part of the population such as epidemics are compensated for by the surplus juveniles from a nearby population.

According to these observations pika minimum population is primarily determined by the factor of forage availability, while the maximum number is controlled by the available territories. As the number of burrows is relatively static, the crucial point in modelling the population dynamics of pika is the implementation of their forage advantage.

3.4.1. Pika's forage advantage

Pika's competitive forage advantage consists of two different features: pika graze more efficiently (Retzer, 2004) and additionally they can extend this advantage into the next year by storing hay for winter. Therefore pika's advantage (fP_{at}) is split into two: the vegetation exclusively available to pika due to their grazing advantage (V_{ag}) and the vegetation exclusively available to them due to the advantage gained by storing this forage as hay (V_{ah}). Pika's competitive advantage subsequently is used to calculate pika's minimum population density (P_m):

$$V_{ag} = V \times fP_{at} \times (1 - fP_{ah}),$$

$$V_{ah} = V_{t-1} \times fP_{ah} \times fP_{at}, \qquad P_m = \frac{V_{ag} + V_{ah}}{fP}$$

As data is lacking, the percentage of pika's advantage realised by storing hay is assigned based on a small set of field data only and therefore somehow arbitrary. However, the effect of varying the percentage of the advantage gained by storing hay (fP_{ah}) is minor.

3.4.2. Territoriality and starvation

As explained above, the number of overwintering adult pika is limited by the number of available burrows (B). Furthermore, pika can die of starvation if forage is scarce. Due to the temporal resolution of 1 year the parallel processes cannot be separated exactly. However, the calculation of the number of pika dying of one of the different causes has to be decoupled to ensure that one individual cannot die twice from different causes. To translate the field observations into model terminology, pika which do not die a natural death of old age either die because they have no burrow for protection or of starvation. In the model the first routine calculated is that for pika dying of predation or exhaustion when they have no territory (=territoriality death, P_{td}). Here, the number of available territories is represented by the number of burrows of the previous year (B_{t-1}) to decouple the processes in time. The number of pika dying of territoriality death can thus be calculated as:

$$P_{td} = P_j \quad \text{if} \ \ P_j > B_{t-1} \times pB^{-1}$$

Subsequently those pika occupying a territory can die of starvation (=death by starvation, P_{sd}) if forage is insufficient ($PCR > 0$). The number of pika actually dying of starvation is therefore calculated according to:

$$P_{sd} = P - P_{td} - P_m \quad \text{if} \ \ PCR > 0 \wedge P_m + P_{td} < P$$

3.4.3. Reproduction of pika

Pika's reproduction is calculated as a net reproduction rate (rP). This linear relationship of the precipi-

tation conditions of the previous 2 years (R_2) and the observed birthrate per ratio of female pika in the population (p) is derived from the conversion of the absolute field observations. The benefit of this approach is that natural death by aging can be neglected

$$rP = (a(rP) + s(rP) \times R_{m2}) \times p$$

The resulting number of juvenile pika P_j is then derived from:

$$P_j = P - P_a$$

3.4.4. Pika population density

The integral change of pika population is finally derived from summarising the single processes in time:

$$\Delta P = P_j - (P_{td} + P_{sd})$$

3.5. Burrow dynamics

The number of burrows (B) limits the adult pika population. Unfortunately there is almost no knowledge on the burrow-digging behaviour of pika. To avoid artefacts it was assumed that the number of burrows observed in the field is representative of the current long-term local phytomass production. Therefore the number of new burrows (nB) is modelled dynamically but fixed within narrow margins. It is assumed that only juvenile pika contribute to the digging of new burrows while adult pika preserve the burrow they inhabit but do not dig new ones. Therefore, burrows decline only if they are uninhabited (B_e). The change in the number of burrows ΔB is derived from:

$$B_e = B - P \times pB \quad \text{if } B > P \times pB,$$
$$\Delta B = nB \times P_j - dB \times B_e$$

4. Results and discussion

4.1. Population dynamics and coexistence

The simulated densities of pika and livestock are shown in Fig. 1. The values for both groups remain within reasonable limits derived from field observations. For example the minimum, mean, and maximum livestock densities in the model are 0.23, 0.61, and 1.58
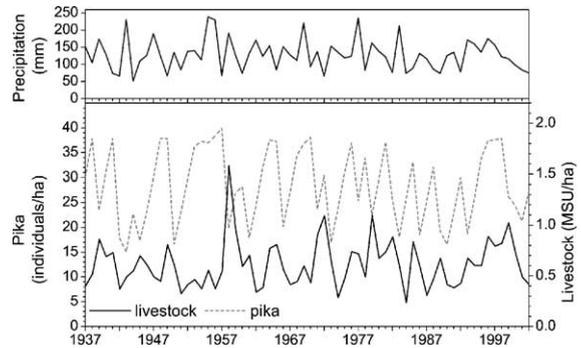

Fig. 1. Simulated densities of pika and livestock from 1937 to 2002. The upper part of the graph depicts the annual precipitation in Dalandzadgad used to drive the model.

MSU, respectively. The mean value of monthly livestock observations from January to September 2001 yielded a monthly minimum density of 0.05, a mean of 0.32, and a maximum of 0.68 MSU/ha. As the year 2001 was characterised by a heavy drought, it seems reasonable that the yearly minimum value of the model is similar, though still slightly lower, than the mean value recorded in the field. Furthermore, it seems reasonable that the maximum monthly average livestock density recorded in June 2001 (0.68 MSU/ha), the only month with at least some precipitation, can be sustained during a whole year with average precipitation and thus justifies the mean annual livestock density of 0.61 MSU/ha simulated in the model. Also the fact that the maximum annual livestock density derived from the model is five times higher than the mean density during a year of drought seems warranted considering the large small-scale variation in livestock densities found in non-equilibrium nomadic systems (Ellis et al., 1993; Desta and Coppock, 2002).

Regarding the dynamics of the pika population, two qualitative criteria are of utmost importance: the population does not become extinct nor does it show mass population outbreaks. The simulated values for pika show a minimum density of 15.0, a mean of 28.3, and a maximum of 39.9. As these figures are mean values of adult pika per year they cannot be compared directly to the number of individuals recorded in the field. However, as far as it can be judged from the available data, these values are also in accordance with the observations of Karin Nadrowski who found approxi-

Table 1
Pearson's coefficients of correlation between the parameters/variables precipitation of current and previous year, simulated densities of pika and livestock, and potential consumption rate (*PCR*)

	PCR	Livestock	Pika	Precipitation
Livestock	0.39[**]			
Pika	0.30[*]	−0.02		
Precipitation	−0.74[***]	0.10	−0.09	
Precipitation previous year	0.17[*]	−0.02	0.16[*]	−0.21[*]

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

mately 30 overwintering adult individuals in the winter of 2000/2001 (Nadrowski et al., 2002). Pika density was considerably lower in the second dry year in a row (Nadrowski, pers. commun.) justifying the minimum value of 15.0 individuals.

4.2. Competition between livestock and pika

The first and seemingly most trivial result of the model is that both groups can coexist in the long term although they feed on the same plant resources. However, the competition has tremendous influence on the population dynamics of both herbivore groups (see Table 1). The correlation between the densities of pika and livestock and the potential consumption rate as an estimator for competition intensity is significantly positive. This is logical as high numbers of herbivores increase the potential consumption rate. Precipitation of the actual year is significantly negative correlated with *PCR* because high precipitation initiates high phytomass production and thus reduces competition. Furthermore, the precipitation of the previous year is positively correlated with *PCR* as high precipitation in 1 year leads to an increase in herbivore densities which in turn face intensified competition the next year when precipitation is usually lower (cf. Desta and Coppock, 2002). The same mechanisms work the other way round. Low precipitation in 1 year leads to a reduction of herbivore numbers and thus competition is reduced when the next year experiences a higher level of precipitation. This pattern is driven by the fact that years with high and low precipitation tend to alternate as can be seen by the significant negative correlation of the precipitation of the actual versus the previous year.
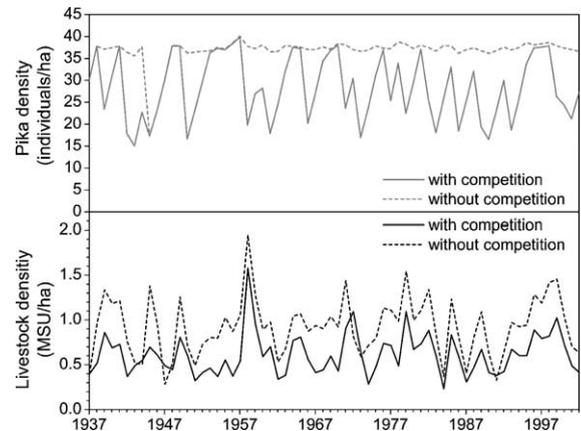

Fig. 2. Densities of pika and livestock in the presence of the other herbivore group (with competition) and in the absence of the other herbivore group (without competition).

However, the three variables livestock, pika, and precipitation are not significantly correlated. This demonstrates the dynamical nature of the model as herbivore densities do not simply run in parallel to the available forage but react sensitively to the competition pressure. Competition affects both herbivore groups. Fig. 2 shows the development of pika and livestock densities under competition and in absence of the other herbivore group. Without competition both the groups increase in abundance: pika from a mean of 28.3 to 36.7 individuals and livestock from 0.61 to 0.93 MSU. Accordingly, the mean potential consumption rate decreases from −0.08 to −0.54 when pika are the only consumers and to −0.15 when livestock are the only herbivore group. Obviously livestock can make better use of the available phytomass than pika whose maximum number is restricted by its need for burrow territories. Although the simulation suggests that the number of livestock can increase in the absence of pika, the effect is not as strong. The figures mentioned above are derived from a simulation run with the number of pika set to zero while all other model components remained unchanged. In the absence of pika, however, their burrows are non-existent as well and the increased phytomass production in these places is no longer available. If this fact is included without pika and their burrows the effect on mean livestock numbers is reduced by half to 0.77 MSU.
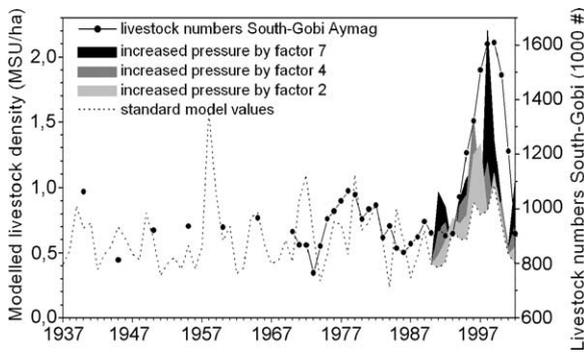
Fig. 3. Probability corridors of 5000 Monte Carlo simulation runs with varying remigration decisions between up to 700% compared to the standard values of the model.

4.3. Transformation

Fig. 3 shows a comparison of the development of the livestock numbers in the South Gobi Aymag and the projected development of livestock densities on the 'balanced model hectare'. Of course the numbers cannot be compared with each other directly. Generally the livestock numbers of the South Gobi Aymag fluctuate much less than those of the model. However, the explanation for this is simple. As the aymag covers an area of 1,654,000 km^2 while the model simulates the variation on one balanced hectare, migration within the aymag due to spatial variation of precipitation can level out many of the extremes experienced at the smaller scale of the 1 ha model plot (Oba et al., 2003). Unfortunately, livestock data on aymag scale from 1935 to 1970 are only available in 5 years intervals. This makes the curve look relatively static in comparison with the years succeeding 1970 but there is no reason to believe that inter-annual variations were smaller during this time.

The precipitation conditions at the beginning of the 1990s were relatively good, but this alone is not enough to explain the tremendous increase in livestock numbers observed during this time (see Fig. 3). Therefore, a simulation run was set up transferring the increasing pressure on the herders to keep higher numbers of livestock to feed a growing rural population. As most herders do not have access to a functioning market the only variable the herders can actually influence is the migration strategy. Therefore, an increased willingness for remigration under good conditions was

implemented to simulate the herders' attempt to exploit the available phytomass even more effectively. This sensitivity simulation runs served to find out whether these changes could explain the observed increases in livestock numbers. Indeed, Fig. 3 shows that a more rigid remigration strategy in combination with a series of years of good rainfall allows herders to exploit the available forage reserves more effectively and livestock numbers can be increased by more than 50%. However, this effect turns out to be only temporary: in relatively favourable precipitation conditions during the 1990s a more intensive stocking system results in higher livestock numbers. But the effect ceases and livestock numbers decrease again dramatically when the period of good weather ends. The high risk strategy (see also Templer et al., 1993 on risk management) takes its toll when three subsequent years of low precipitation (2000–2002) reduce the livestock numbers back to pre-transformation level—in reality as well as in the model (Fig. 3). This collapse of the livestock populations indicates that changing the migration strategy is not a long-term option.

The management is near the optimum and cannot be intensified further without violating the boundaries of the system.

The series of rainfall events in the 1990s is an exception to the long-term distribution of precipitation intensities: This time span is characterised by above-average precipitation levels with relatively low inter-annual variability. For example from 1993 to 1997, precipitation was above average. Since the beginning of recordings in Dalandzadgad this was the first time that five subsequent years received above-average precipitation. Also, extreme events occurred only rarely: during the 1990s the deviation of the precipitation of each year was constantly less than 40% of the mean. In the five previous decades extreme years with more than 40% deviation from the mean occurred at least twice, on average 3.6 times, and at most 6 times per decade! In 1998 and 1999 the situation changed. In both years a slightly below-average precipitation was recorded (−5% and −9%). The years 2000–2002 all received well below-average precipitation (−24%, −35%, and −41%, respectively). Again, five subsequent years with below-average precipitation in a row have not been recorded previously.

As shown from the precipitation data the situation in the 1990s was much more an equilibrium-

situation than in the decades before. Especially the absence of years with precipitation well below average, which usually efficiently decreased livestock numbers every few years, allowed the build-up of high livestock numbers. For 5 years livestock numbers could grow continually until the growth was halted by average conditions in 1998 and 1999. Finally the risk of stocking a non-equilibrium system according to equilibrium conditions took its toll: the increased livestock numbers could not be maintained in the bad conditions of 2000–2003 and a high proportion of livestock died in the dzud[1] of 2000–2003 (National Statistical Office of Mongolia, 1996, 1998, 2000, 2001, 2002, 2003).

The consequence of the observed and simulated patterns for the long-term carrying capacity is clear: the relatively good distribution of precipitation in the 1990s allowed a large number of Mongolians to escape the hardships of a collapsing state by living self-sufficiently from their herds (Janzen and Bazargur, 2003). But it cannot be expected that the carrying capacity can be expanded much beyond what has been already realised in the 1930s–1980s. This also means that the number of people living from herding in Mongolia cannot increase in the long term, either. The population of Mongolia can only increase further sustainably if other means of earning their livelihood become more and more available (Janzen, 2000). Pastoral nomadism could absorb a part of the shock from the transformation, but will not feed a substantially higher number of people in future.

4.4. Outlook

As shown above, amount and distribution of the precipitation are crucial to the functioning of the system. The 1990s were an exception to the previous recordings. Yet, it cannot be distinguished whether this was a mere coincidence, or whether these are first signs of changed precipitation patterns in the context of climate change. Bolortsetseg and Tuvaansuren (1996) predict negative effects for the pasture production in the Gobi desert area because increasing temperatures may lead to a general decline in livestock intake and average daily weight gain especially in late summer.

If phases of good precipitation, as observed in the 1990s, become more frequent, this will alter the dynamics driving Mongolian pastoralism towards a more equilibrial system. This implies that livestock numbers will much more frequently be near the 'actual carrying capacity' (see Behnke et al., 1993) and much more seldomly clearly below it. Under such conditions the questions of potential overgrazing and regulations of pasture use become much more important than previously to avoid degradation.

Further investigations will account for long-term precipitation datasets (dendrochronology) as well as future climate simulations as derived from ECHAM4 (Roeckner et al., 1996). While the long-term precipitation dataset will provide a better understanding of the sensitive variables and dynamics of the model, the latter approach will be applied to investigate the utility of the model for investigations of climate change-related scenarios. The model is suited to investigate the effects of climate change projections on the precipitation patterns in Mongolia by using the results of climate simulations as precipitation input parameters. Further changes in temperatures, however, have to be considered indirectly via their effect on the rain use efficiency of the vegetation.

Furthermore, we plan to develop a spatially explicit model based on the model presented here. It will incorporate vegetation dynamics derived from satellite images (NDVI) and will explicitly address migration strategies employed by the herders to investigate the impact of herder mobility on large-scale carrying capacity.

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[1] Dzud is a Mongolian term describing severe winter weather causing episodic mortality in herbivore, especially livestock populations (see also Begzsuren et al., 2004).

Appendix A. Model initial values, runtime variables, and constants

Variable	Description	Dimension	Value
b	Average burrow area in percentage of model hectare	dmnl	0.0032
B	Number of burrows (initial value 30)	dmnl	rt
B_A	Percentage area of the model hectare covered with pika burrows: $B_A = B \times b$	dmnl	rt
B_e	Number of empty burrows	dmnl	rt
dB	Factor of empty burrows decaying	dmnl	0.0005
nB	Factor of burrows built per juvenile pika	1/individual	0.001
pB	Number of burrows per pika (1 due to territoriality)	1/individual	1
F_L	Potential forage demand of actual livestock population $= fL \times L$	kg	rt
F_P	Potential forage demand of actual pika population $= fP \times P$ (see also Appendix B)	kg	rt
F_d	Forage deficit	kg	rt
mH	intensity of herders' emigration wish	dmnl	rt
$a(mH)$	y-intercept of mH linear relationship	dmnl	1
$s(mH)$	Slope of mH linear relationship	dmnl	0.7
rH	Intensity of herders' immigration wish	dmnl	rt
$a(rH)$	y-intercept of rH linear relationship	dmnl	1
$s(rH)$	Slope of rH linear relationship	dmnl	0.7
L	Number of livestock (initial value 0.4)	MSU	rt
L_m	Number of emigrating livestock	MSU	rt
L_r	Number of immigrating livestock	MSU	rt
L_{rp}	Number of born livestock ("reproduced")	MSU	rt
L_{sl}	Number of slaughtered livestock	MSU	rt
L_{st}	Number of starving livestock	MSU	rt
fL	Forage intake per year and livestock	kg/MSU	365
stL	Factor of livestock starvation	dmnl	0.4
mL	Factor of livestock emigration	dmnl	rt
rpL	Reproduction rate of livestock (see also Appendix B)	dmnl	rt
slL	Livestock slaughter rate (see also Appendix B)	dmnl	rt
stL	Livestock starvation rate	dmnl	rt
P	Ratio of female pika	dmnl	0.6
P	Number of pika (initial value 30)	Individual	rt
P_a	Number of adult pika that survived winter in their burrows: $P_a = \frac{B_{t-1}}{pB}$	Individual	rt
P_j	Juvenile pika	Individual	rt
P_m	Pika's minimum population sustained by their competitive forage advantage	Individual	rt
P_{sd}	Number of starving pikas	Individual	rt
P_{td}	Pika mortality due to territoriality constraints	Individual	rt
fP	Forage intake by pika	kg/individual	5
fP_{ah}	Percentage of pika's total forage realised by hay stocking	dmnl	0.1
fP_{at}	Pika's total competitive forage advantage (percentage from available biomass)	dmnl	0.21
rP	Reproduction rate of pika	dmnl	rt
$a(rP)$	y-intercept of rP linear relationship	dmnl	0.2
$s(rP)$	Slope of rP linear relationship	dmnl	0.2
PCR	Standardised potential consumption ratio	dmnl	rt
r	Mean precipitation of time serie	mm	131
R	Annual precipitation of Dalandzadgad	mm	Data
R_n	Average of the previous n years precipitation: $\sum_{t=0}^{n} \frac{R_t}{n}$	mm	rt
R_{2s}	Standardised deviation of the previous 2 years' precipitation from the long-term mean: $\frac{R_{t-1} + R_{t-2}}{2r}$	dmnl	rt
RUE	Rain use efficiency of the vegetation (=production of dry phytomass per mm precipitation)	kg/mm	rt
$rue\,S$	Rain use efficiency of the steppe matrix, which is the production of phytomass per mm precipitation	kg/mm	3.22
S_A	Percentage of area with steppe vegetation: $S_A = 1 - B_A$	dmnl	rt
t	Time	yr	rt
v	Constant of vegetation biomass not available to herbivores	kg	30
V	Net vegetation biomass	kg	rt

Appendix A (*Continued*)

Variable	Description	Dimension	Value
V_{ag}	Growing vegetation biomass exclusively available for pikas	kg	rt
V_{ah}	Vegetation biomass exclusively available for pikas as hay from the previous year	kg	rt
V_e	Vegetation biomass estimated by the herders from their knowledge on previous precipitation prior to migration	kg	rt
bV	Factor of higher productivity of vegetation biomass on pika burrows	dmnl	2.9

Appendix B. Parameters of the Gauss normally distributed filter functions

Variable	Minimum	Maximum	Mean	Standard deviation
gF_d	$F_d - 0.5 \times F_d$	$F_d + 0.5 \times F_d$	F_d	50
rpL	0.15	0.4	0.3039	0.0414
slL	0.2	0.36	0.284	0.032

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