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# Surviving a Drought: Population Dynamics of *Ochotona pallasii pricei* in a Dry Steppe, Gobi Altai, Mongolia


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## Surviving a drought: population dynamics of *Ochotona pallasii pricei* in a dry steppe, Gobi Altai, Mongolia

K. Nadrowski & G. Miede

*Nomenclatural reference: Scientific names of small mammals follow SOKOLOV & ORLOV (1980)*

### Abstract

Two distinct life history traits are described from the genus *Ochotona*, the group of “burrowing” species exhibiting high but fluctuating population densities and the “non-burrowing” species exhibiting relatively stable low population densities. The life history traits are linked to ecosystem dynamics with climatically variable steppe environments hosting “burrowing” species and relatively stable mountainous and rocky habitats hosting “non-burrowing” species. There are few intermediate species, living in both steppe and rocky environments. This study presents survival rates, reproductive rates and a tentative model of population dynamics for *Ochotona pallasii pricei*, an intermediate species with respect to habitat preference. We used Cormack-Jolly-Seber models on 153 trapped as well as observed individuals during 10 encounter occasions to estimate survival rates. The study period lasted from November 2000 to July 2002, including a severe drought summer in 2001. Reproductive rates are estimated based on observation of the 100 x 100 m<sup>2</sup> study site. Population dynamics are simulated using a Leslie-Matrix with monthly time steps. Neither the drought conditions nor the harsh winter conditions showed an influence on the survival rates of the observed individuals. Instead, population density, sex, and age were explaining factors in the most parsimonious model. Independence of climatic conditions suggests that *O. pallasii pricei* exhibits traits of a “non-burrowing” species although living in a variable steppe environment. This sheds new light on the evolution of the behavioural traits of pikas, since the variability of the climate cannot predict the life history traits of the species. The behavioural traits may be more conservative than has been assumed previously. Survival during the drought summer is probably enabled by the storage of enough dry herbs and grasses in the burrows of the animals, while the territorial behaviour of the species is the prerequisite of harvesting enough biomass to persist through the adverse climatic conditions of a potentially coming drought.

**Keywords:** *Ochotona*, life history, ecosystem dynamic, burrowing, population dynamics, model

### Introduction

Climatic variability is a major force controlling the population dynamics of organisms in arid environments, where opportunistic and less stable population dynamics prevail (WIENS 1984). Within the genus *Ochotona*, SMITH (1988) and SMITH et al. (1990) distinguish between two distinct suites of life history traits, which are still used in recent literature (YU et al. 1997, 2000): the “burrowing” species live in non-equilibrium systems which show high climatic variability, while the “non-burrowing” species live in systems showing relatively less climatic variability. “Burrowing” pikas generally live in steppe environments, while “non-burrowing” pikas occur in rocky habitats. “Non-burrowing” pikas are relatively asocial and comparatively long-lived, and have relatively stable low population densities and low fecundity rates. In contrast, “burrowing” pikas normally are highly social and short-lived, and have high but fluctuating population densities and high fecundity rates (SMITH 1988, SMITH et al. 1990). In Asia, the “burrowing” type of pikas can become a small mammal pest species, and pikas are controlled in China and formerly in Mongolia and Russia regardless of the population dynamics exhibited (SMITH & FOGGIN 1990, ZHONG et al. 1985).

*Ochotona pallasii*, the Pallas' Pika, has been labelled as intermediate in habitat preference, occupying both rocky and steppe biotopes, but is a “burrowing” pika according to its life history



traits following SMITH (1988). There is little information available on this species; and none of the previous studies employed a mark-recapture methodology to follow the fate of living individuals (SMITH et al. 1990, SHUBIN 1966, KRYLOVA 1973).

This study therefore focuses on factors controlling survival rates and simulates a population dynamic based on reproduction and survival of *Ochotona pallasi pricei*, the Mongolian pika, from a dry steppe system exhibiting non-equilibrium dynamics including a summer of drought.

## Methods

### Study area

The study was performed in the Gobi of southern Mongolia (fig. 1, 2), at 43°36.949'N, 103°46.45'E. The study site is part of the Gobi Gurvan Saikhan National Park (GGS NP), but virtually the entire area is under permanent and complete anthropo-zoogenic influence (READING et al. 1999, MIEHE 1998, STUMPP et al. 2005). The landscape comprises the south-easternmost outcrops of the Gobi Altai (summits up to 2900 m asl), which are surrounded by vast pediments extending from 2300 m down to some 1200 m asl. The study site is located on the upper pediments at 2350 m asl with a southern exposure and a low inclination (6°).

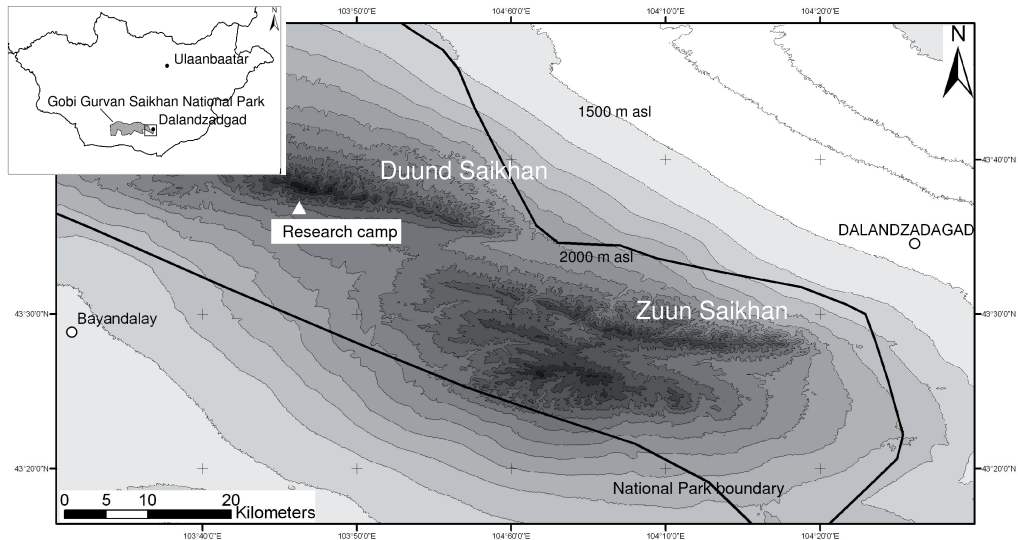


Fig. 1: Location of the research camp in the eastern part of the Gobi Gurvan Saikhan National Park, Mongolia.

Bayandalai, a governmental weather station some 30 km SW of the study area (1500masl) reports a long-term mean annual temperature of 4.5 °C (January -18 °C, July 20 °C), while mean precipitation is 110 mm with a high coefficient of variation (around 35 %; RETZER 2004). Precipitation increases with altitude. Short-term measurements between 2000 and 2300 m asl indicate higher, but equally variable, precipitation levels: 72 mm for the drought year 2000/2001 (RETZER 2004), 126 mm for 2003/2004 and 125 mm for 2004/2005 (WESCHE et al., in press). Precipitation falls mainly in summer, and its variability has a pronounced effect on the production of standing biomass (WESCHE et al., in press).

At 2000 m - 2600 m asl, montane steppes with *Stipa krylovii*, *S. gobica* and *Allium polyrrhizum* represent the dominant vegetation (WESCHE et al., 2005). The study site is typical for this habitat with respect to vegetation, soil conditions, and remote sensing characteristics (WESCHE et al., in press). These steppes represent the most important pastures in the region; they are intensively used by both domestic livestock and small mammals, with pikas (*Ochotona spec.*) being the most important group (NADROWSKI 2006).

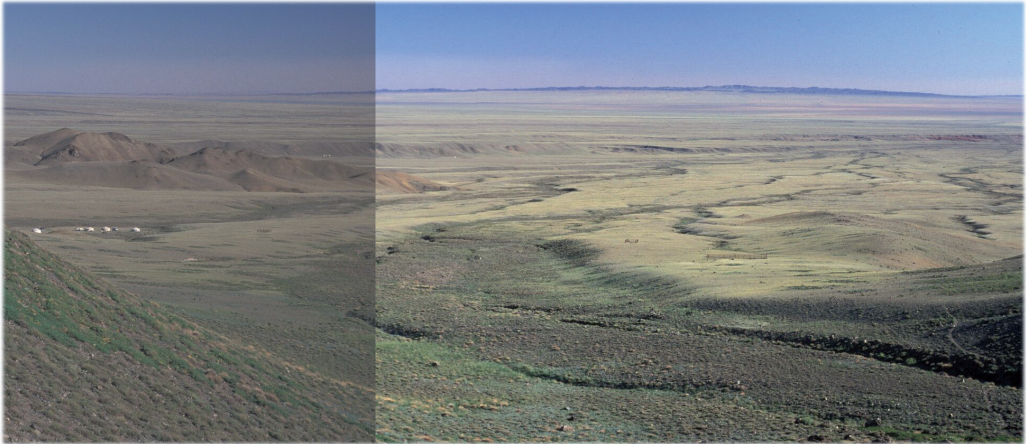


Fig. 2: View of the research camp to the left and the study site to the right on the upper part of the pediments of the Duund Saikhan mountain. The panorama is made of two different pictures, center direction is south. Taken in summer 2002.

### Study species

Ochotonidae are endemic to the modern Holarctic Region. Most of the species are confined to either high latitudes or high altitudes. In the study region, two species occur, namely *Ochotona daurica* and *O. pallasii pricei* (NADROWSKI 2006). They are among the most drought-tolerant pika species with *O. daurica* being widespread in Mongolian grass steppes, while *O. p. pricei* is found in dry mountain steppes and desert steppes of the Mongolian and Gobi Altay (SMITH et al. 1990). *Ochotona pallasii pricei* is the most common species in the montane steppes of the GGS NP (NADROWSKI 2006). Its centre of abundance is in the altitudinal range 2200 – 2800 m asl, where it occurs in the montane steppes and moist desert steppes described above (NADROWSKI 2006; estimated total range ca. 600 km<sup>2</sup> in the GGS NP according to spatial data by H. v. WEHRDEN).

Although *Ochotona p. pricei* occurs both in rocky habitat and steppe habitat and is thus labelled “intermediate” with respect to habitat selection (SMITH 1988, SMITH et al. 1990), it has been assigned to the “steppe dwelling” pikas according to its life history parameters by SMITH (1988). Reproductive rates as well as density variation are reported to be high, while survival rates on this species have not been studied yet.

### Data collection

Animals were captured and observed on a 100 x 100 m<sup>2</sup> study site. A 10 x 10 m<sup>2</sup> grid was established by piling stones at the edges of the grid to aid orientation. Sherman life traps (www.shermantraps.com) of two sizes were used for capture, Extra Large (10 x 12 x 38 cm) and Large (8 x 9 x 23 cm), although only Extra Large traps should be used in further studies. Baiting was not needed to capture animals. Animals were identified using SOKOLOV & ORLOV (1980). Individuals were observed from within a car with binoculars. Capture sessions consisted of several subsequent trapping sessions and lasted for 2 to 3 days, while observation sessions lasted 2 to 7 hours. The study site was observed until no new animals could be detected. Animals were marked using ear tags (Mini-Ohrmarken, Tierzuchtgeräte-Strietzel, Günthersleben, Germany), but further use of these ear tags for pikas is not recommended. See KAWAMICHI & LIU (1990) for instructions on tagging pikas. Animals were additionally marked by dyeing their hair with picric acid. Identification success of capture (97.6 %) and observation (97.1 %) is similar and high (NADROWSKI 2006).

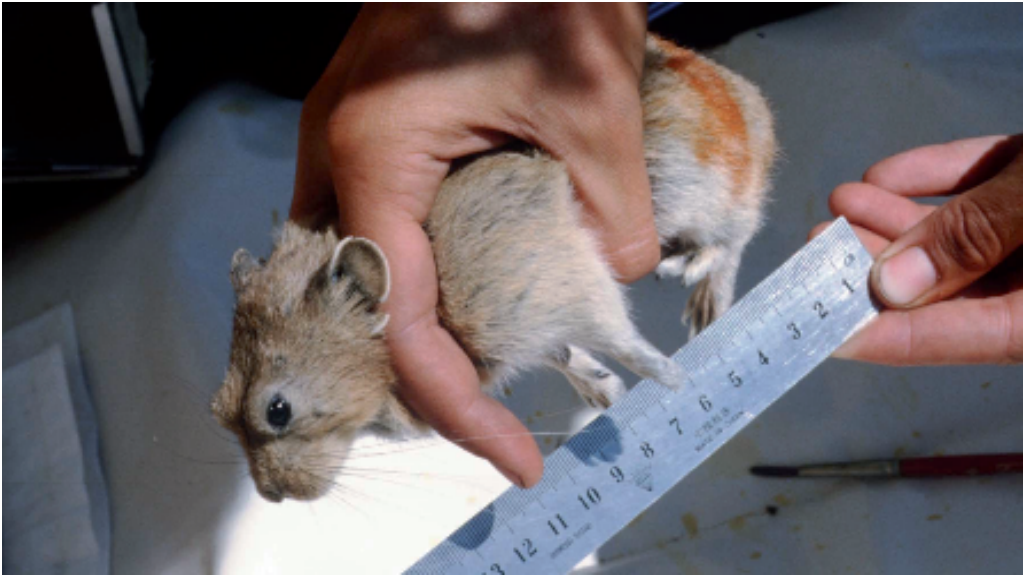


Fig. 3: Holding an individual of *Ochotona pallasi pricei* during handling. Hair dyed with picric acid is seen on the hind legs of the individual.

Ten joint capture and observation sessions were used for this analysis, starting in November 2000 and ending in July 2002 (table 1). A total of 153 individual Mongolian pikas can be compared to identify factors influencing survival rates.

Reproductive rates are estimated based on the observation of juveniles on the study site in the year 2001. Juveniles were allocated to the burrow they were first observed on. Additionally, adult females were allocated to the burrows. The maximum number of juveniles per adult female is used as maximum reproductive rate in the simulation.

### *Data analysis*

Survival rates are evaluated by the analysis of the mark-recapture data. Cormack-Jolly-Seber models (CORMACK 1964, JOLLY 1965, SEBER 1965) as implemented in the software MARK (WHITE & BURNHAM 1999) consider reencounter and survival probabilities. These models make the assumption that (1) each individual from a selected group of individuals has the same probability of survival from time  $t$  to  $t+1$ . Furthermore, these models assume (2) that the individuals are identical in their probability of being reencountered at time  $t+1$  (LEBRETON 1992). After checking the full model with Chi-Square tests and bootstrapping methods, a candidate set of models is compared to evaluate the influence of climatic effects, population density, age, and sex on survival and recapture probabilities (WHITE & BURNHAM 1999). Models are compared using an adapted Akaike's information criterion (QAIC<sub>c</sub>), which weighs the model deviance and the number of parameters used. The currently accepted convention is that models with QAIC<sub>c</sub> that differ by  $< 2$  are indistinguishable in terms of their fit to the data (BURNHAM & WHITE 2002). The most parsimonious model has the highest QAIC<sub>c</sub> weight.

Variables tested are time of encounter occasion, cohort, population density, and sex. The encounter occasions can be grouped to depict the drought and a winter and a summer season (table 1). Cohort affiliation was reconstructed using a dynamic weight criterion based on observed growth curves (NADROWSKI 2006). For a given cohort, the age at a given time of encounter is the same (table 1). Age is given as an ordinal variable with the ranked categories "juvenile", "adult", "senior".

Table 1: Parameter coding for modeling survival rates. Precipitation ( $p$ ) indicates the time of the drought (1 for the months which experienced the drought), while season ( $w$ ) is given as winter ( $w$ ), summer ( $s$ ) and an extra category ( $e$ ) for the interval between September 2001 and July 2002. Population density is given in individuals/ha. The age for the individuals in the different cohorts consists of the categories junior ( $j$ , first summer), adult ( $a$ , first winter to third summer), and senior ( $se$ , from the third winter on).

	Month of capture occasion									
	2000		2001						2002	
Model notification	11	01	04	05	06	07	08	09	07	07
Precipitation ( $p$ )	0	0	0	1	1	1	1	1	0	0
Season ( $w$ )	w	w	w	s	s	s	s	e	s	s
Density ( $d$ )	20.6	22	19.8	19.8	46.1	26.2	21.1	22.4	14.6	16.3
Age										
Cohort 1999	a	a	a	a	a	a	a	se	se	se
Cohort 2000	a	a	a	a	a	a	a	a	a	a
Cohort 2001	-	-	-	j	j	j	j	a	a	a
Cohort 2002	-	-	-	-	-	-	-	-	j	j

A total of 30 models are compared modelling different hypotheses regarding recapture and survival probabilities. For modelling recapture rates, an influence of age, season, population density, and sex is assumed. Time is grouped in season and age, season and density, and season, age and density. Then season is left out, while in the following models age, density, and the combination of age and density are left out, resulting in a model only featuring sex as explaining variable. The most parsimonious version of this model run is then further reduced by taking out the interactions and each of the main effects. For modelling survival rates the most parsimonious model resulting from the previous run is further simplified. An additional quadratic influence of age is assumed, plus the influence of the drought summer and a cohort effect (table 1). Similar to the recapture models, time is replaced by season and drought, while age replaces time and cohort. The most parsimonious model is again simplified by taking out the interactions and leaving out each main effect.

30 day survival rates are extracted from the most parsimonious model and used together with reproductive rates to simulate the population density of the pikas. This is done using Leslie-matrices, which calculates the number of individuals from one discrete time step to the next based on fertility and survival rates (KREBS 1999). The fertility rates ( $f$ ) combine reproduction per adult female ( $b$ ) and survival to the next time step of the newborn juveniles ( $s_j$ ):  $f = bs_j$ .

For females the formula thus reads  $f_F = b_F s_{F,j}$  and for males  $f_M = b_M s_{M,j}$ .

The matrices used in the simulation have the following form, where the number of females in the next time step is determined by the fertility ( $f$ ) and survival rates ( $s$ ) of females:

$$\begin{bmatrix} F_{0.5,t+1} \\ F_{1.0,t+1} \\ F_{1.5,t+1} \\ F_{2.0,t+1} \\ F_{2.5,t+1} \\ F_{3.0,t+1} \\ F_{3.5,t+1} \end{bmatrix} = \begin{bmatrix} 0 & f_F & 0 & f_F & 0 & f_F \\ s_{F,a} & 0 & 0 & 0 & 0 & 0 \\ 0 & s_{F,a} & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{F,a} & 0 & 0 & 0 \\ 0 & 0 & 0 & s_{F,a} & 0 & 0 \\ 0 & 0 & 0 & 0 & s_{F,a} & 0 \end{bmatrix} \begin{bmatrix} F_{0.5,t} \\ F_{1.0,t} \\ F_{1.5,t} \\ F_{2.0,t} \\ F_{2.5,t} \\ F_{3.0,t} \\ F_{3.5,t} \end{bmatrix}$$

The number of male juveniles is determined by the fertility rates for the males ( $f$ ) which is again dependent on the number of adult females present, while the number of male adults is dependent on the survival rates of adult males ( $s$ ):

$$\begin{bmatrix} M_{0.5,t+1} \\ M_{1.0,t+1} \\ M_{1.5,t+1} \\ M_{2.0,t+1} \\ M_{2.5,t+1} \\ M_{3.0,t+1} \\ M_{3.5,t+1} \end{bmatrix} = \begin{bmatrix} 0 & f_M & 0 & f_M & 0 & f_M \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} F_{0.5,t} \\ F_{1.0,t} \\ F_{1.5,t} \\ F_{2.0,t} \\ F_{2.5,t} \\ F_{3.0,t} \\ F_{3.5,t} \end{bmatrix} + \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ s_{M,a} & 0 & 0 & 0 & 0 & 0 \\ 0 & s_{M,a} & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{M,a} & 0 & 0 & 0 \\ 0 & 0 & 0 & s_{M,a} & 0 & 0 \\ 0 & 0 & 0 & 0 & s_{M,a} & 0 \\ 0 & 0 & 0 & 0 & 0 & s_{M,a} \end{bmatrix} \begin{bmatrix} M_{0.5,t} \\ M_{1.0,t} \\ M_{1.5,t} \\ M_{2.0,t} \\ M_{2.5,t} \\ M_{3.0,t} \\ M_{3.5,t} \end{bmatrix}$$

The simulation uses months as time steps. Reproduction is simulated as one event before summer; summer consists of four months, while winter consists of 10 months.

## Results

Although both, the climate-related variables drought ( $p$ ), season ( $w$ ), and cohort ( $c$ ) and population density ( $d$ ) are included in the ten most parsimonious models shown in table 2, the two models with the highest QAIC<sub>c</sub> weight only include population density apart from age and sex to explain the survival and recapture rates of the sampled individuals, and none of the climate-related variables.

Table 2: The ten most parsimonious models of the survival ( $\varphi$ ) candidate set. Model descriptors are the information criterion QAIC<sub>c</sub> and the QAIC<sub>c</sub> weight, which sums to one for all models tested; the number of parameters (K) and the deviance of the model. Model parameters are sex ( $s$ ), cohort ( $c$ ), time ( $t$ ), season ( $w$ ), drought ( $p$ ), age ( $a$ ), and density ( $d$ ).

Model rank	Model parameters	QAIC <sub>c</sub>	QAIC <sub>c</sub> weight	K	Deviance
1	$\varphi(s,a,d)$	442.96	0.690	10	197.6
2	$\varphi(s+a+d)$	445.70	0.154	6	208.8
3	$\varphi(s,c,d)$	448.23	0.044	12	198.5
4	$\varphi(s,a)$	448.73	0.034	7	209.7
5	$\varphi(s,p,a,d)$	449.15	0.028	14	195.0
6	$\varphi(s,c,w,d)$	449.42	0.024	18	186.3
7	$\varphi(s,c,w,p,d)$	449.50	0.023	19	184.1
8	$\varphi(s,p,a)$	449.74	0.020	10	204.4
9	$\varphi(s,c,t)$	450.62	0.013	23	175.9
10	$\varphi(s,c,p,d)$	451.21	0.010	16	192.6

Although sample size does not allow estimating all of the combinations of density, age, and sex, 30 day survival rates tend to decrease with density, the only exception being the male adults. Female survival tends to be greater than male survival and adult survival greater than juvenile survival (fig. 4). Since adult male survival has a large standard error for low densities and cannot be estimated for high densities, it is assumed to be constant for the following simulation of population density.

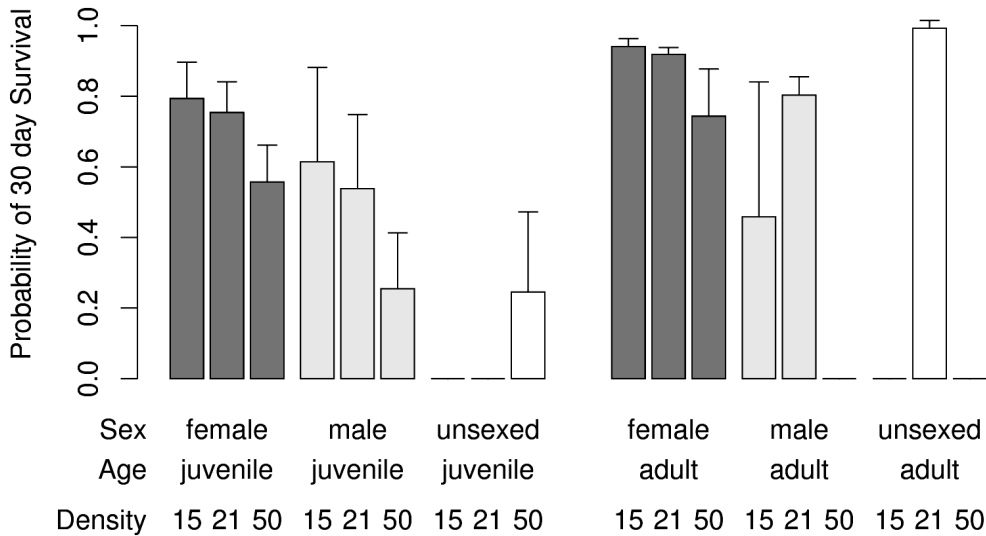


Fig. 4: Parameter estimates for 30 day survival probabilities of the most parsimonious model according to table 2. Survival probabilities are dependent on sex (female, male, and unsexed individuals), age (juvenile and adult individuals as shown in table 1; the senior age category could not be estimated due to the small sample size), and population density measured in individuals per hectare and ranging between 15 and 50 individuals per hectare.

Reproduction could be observed on 17 out of 29 burrows by the appearance of juveniles. Median number of juveniles per burrow was three. There was one case of two litters on one burrow and one case of two litters of one female, distributed on two burrows. This female had the maximum of 13 juveniles on her burrows. The following simulation thus uses 13 juveniles per female as maximum reproductive rate. It is assumed that the proportion of female and male offspring is the same, so the resulting reproductive rate ( $b$ ) is 6.5 female and 6.5 male juveniles per adult female individual.

Data on survival probabilities and reproductive rate result in the following equations for simulating population densities. While the rate of reproduction is assumed to be constant per adult female as described above, the survival rate ( $s$ ) depends on population density ( $d$ ), age, and sex, reflecting the explaining variables of the most parsimonious model described above. The fertility rate ( $f$ ) integrating reproduction ( $b$ ) and juvenile survival ( $s$ ) thus is

$$\text{for female juveniles} \quad f_F = bs_{F,j} = 6.5 (0.87 - 0.40d - 0.44d^2)$$

$$\text{and for male juveniles} \quad f_M = bs_{M,j} = 6.5 (0.80 - 1.16d - 0.17d^2),$$

$$\text{while adult female survival } (s_{F,a}) \text{ is given by} \quad s_{F,a} = 0.96 + 0.04d - 0.93d^2$$

$$\text{and adult male survival } (s_{M,a}) \text{ is assumed to be constant at} \quad s_{M,a} = 0.802.$$

The simulation of population densities results in a stable but oscillating attractor for each of the starting points of the four trajectories. Starting with one female and one male individual, a population density of 25 females and 11 males after the summer and a density of 8 females and 2 males after the winter is reached in the third year simulated (fig. 5). For the other starting points the attractor is reached even earlier. This results in population densities oscillating between 36 and 10 animals on one hectare.

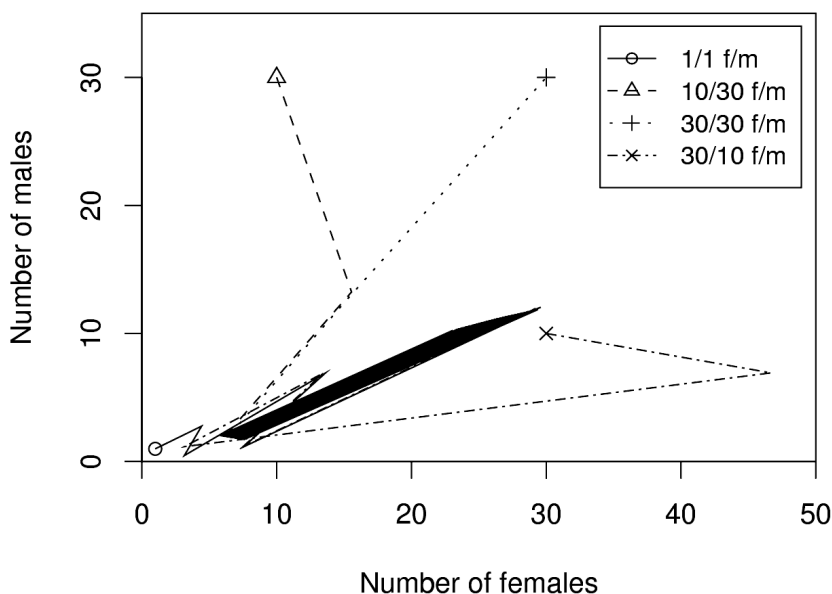


Fig. 5: Trajectories for the number of females and the number of males on a hectare steppe as simulated by the Leslie-matrices. Trajectories of four starting points are visualized; the ratio of female to male (f/m) individuals of the starting points is given in the legend.

## Discussion

The finding that survival probabilities are independent of climatic variables is surprising given that a small mammal living in a non-equilibrium ecosystem was studied. WIENS (1984) shows that in non-equilibrium systems, organisms tend to have more opportunistic and less stable population dynamics. SMITH (1988) and SMITH et al. (1990) elaborate the same pattern for the genus of pikas, showing that steppe-dwelling species have life history traits leading to strongly fluctuating population densities susceptible to climatic variation while species found in other habitats show stable population densities. In pikas, steppe-environments thus represent the non-equilibrium environments in contrast to the other habitats pikas are found in, such as alpine ecosystem, forests, or scrub. Thus, finding *Ochotona pallasi pricei* in the montane steppes of the Gobi Altai to exhibit populations dynamics independent of climatic variables seems to contradict the distinction between steppe-dwelling and other pikas. At the same time, independence of climatic variation as shown here and relatively low reproductive rates as compared to other pika species (NADROWSKI 2006) fits well in the group of non-burrowing pikas living in non-steppe environments as described by SMITH (1990). Thus, the Mongolian pika exhibits traits of pikas from non-steppe ecosystems while living in a steppe ecosystem.

Accepting the link between non-equilibrium ecosystem dynamics and opportunistic life history traits, this contradiction might imply that a) the Mongolian pika has not evolved in the present steppe environment and is thus not adapted to this environment or b) the species has means at its disposal to mitigate the effect of climate variation.

### *The Mongolian pika is not adapted to steppe environments*

Pika species living in steppe environments are called “burrowing”-species since they erect their own burrows (SMITH 1990). These species feature relatively long claws and vibrissae. The Mongolian pika in the contrary does not have the long claws characteristic for other burrowing pika species (ZEVEGMID 1975), although it constructs burrows. Burrowing activity is low in the Mongolian pika though, where burrows are used for many generations (NADROWSKI 2006).

A behavioural trait typical for steppe-dwelling pikas is their social behaviour with frequent friendly interactions between neighbouring individuals (SMITH 1988, SMITH et al. 1990). The Mongolian pika in the contrary shows aggressive behaviour towards other pikas (PROSKURINA et al. 1985).

A karyological study of eight taxa of pikas suggests that the steppe-dwelling pikas (*Ochotona pusilla*, *O. daurica*, *O. pallasii pricei*) have entered the steppe environment at three independent times (VORONTSOV & IVANITSKAYA 1973, quoted in YU et al. 1997), so that it may be possible that *O. pallasii pricei* entered the steppe environment later than the other species and thus does not show the adaptations. On the other hand, processes on a larger time scale may be responsible for the differences between the two suits of life history traits in pikas. YU et al. (1997) and YU et al. (2000) suggest that the genus experienced a rapid radiation in the late Pliocene and early Pleistocene, caused by the uplifting of the Tibetan (Qinghai-Xizang) Plateau. This led to colder and, especially in the rain-shadow of the Himalaya massif, dryer conditions. Climatic oscillations with glacial and interglacial transitions, but without a unified ice-sheet, resulted in continual habitat shifts on the Tibetan Plateau. In contrast to this, the ecosystems north of the Tibetan Plateau experienced relatively less dramatic changes. YU et al. (2000) suggest three subgeneric groups for the genus *Ochotona*, a shrub-steppe group and a mountain group, both originating from the Tibetan Plateau, and a northern group, originating from the ecosystems north of the Plateau. They list all the species of the shrub-steppe group as “burrowing” pikas (including *O. thibetana*, *O. annectens*, *O. cansus*, *O. curzoniae*, *O. nubrica*, *O. daurica*, *O. thomasi*), while all species of the northern group except for *O. pallasii* are listed as non-burrowing pikas (including *O. hyperborea*, *O. alpina*, *O. pallasii* (not subspecies *pricei*), *O. princeps*). *Ochotona pallasii* is listed as intermediate species. The third group contains species which exhibit both burrowing and non-burrowing characters. From the results presented here, the studied subspecies *O. pallasii pricei* can be classified as “burrowing” species in respect to its population dynamics. This supports the idea that the two groups derived by YU et al. (2000) based on molecular data are homogeneous in regard to their life history traits. Thus, the behavioural traits leading to a “burrowing” or a “non-burrowing” life history may not have developed more than once, as suggested by SMITH (1988) and SMITH et al. (1990). Additionally, these behavioural traits are independent of the present ecosystem type, since *O. pallasii pricei* exhibits these traits in a dry steppe environment. But nonetheless with a lifespan of about two years (NADROWSKI 2006) between-year climatic variations and associated variations in food availability must still be important for the Mongolian pika. To succeed in such an environment the species must have means at its disposal mitigating the effect of climatic variation.

### *Mitigating climatic variability*

Ecosystem processes in the study area are essentially governed by non-equilibrium dynamics: standing crop is controlled by precipitation and not by herbivore grazing (WESCHE & RETZER 2005, RETZER 2005b) and the composition of the vegetation is not influenced by the Mongolian pika (NADROWSKI 2006). While standing crop increased during the summer 2000, it decreased during the drought summer 2001 (RETZER 2004). At the same time, individual survival rates of pikas are not affected by the drought conditions (table 2).

A possible explanation for this observation is the presence of stored food in the burrows of the pikas. Since pikas store food for the winter (SMITH et al. 1990), this may have lasted through the following summer of drought in 2001. Taking this as a reason for the high survival rates, it still needs to be explained why it is possible for a single individual to gather enough grasses and herbs during one summer. This again can be explained by their territorial behaviour (PROSKURINA et al. 1985, MONKHZUL 2005). The possession of a sufficiently large territory is thus a prerequisite of harvesting enough biomass to possibly survive through adverse climatic conditions in the coming summer. Thus, the difference between the population dynamics exhibited by “burrowing” and “non-burrowing” pikas may be primarily a behavioural difference, based on the territoriality. More information is needed on the behavioural differences of pika species and especially *O. pallasii* subspecies to discern the influence of ecosystem quality on different time scales for the evolution of their life history traits.



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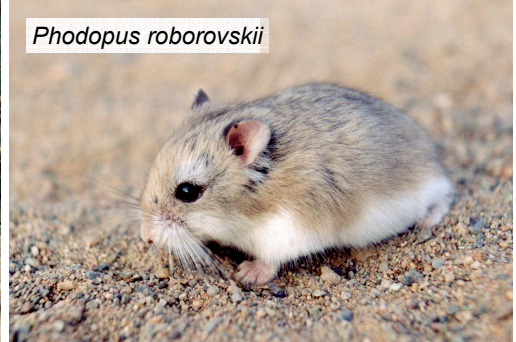
*Ochotona pallasii*



*Citellus erythrogenys*



*Meriones unguiculatus*



*Phodopus roborovskii*



*Salpingotus kozlovi*



*Dipus sagitta*



*Allactaga bullata*



*Cardiocranius paradoxus*

Small mammal species of desert and semi-desert communities (photos: A. & M. STUBBE).