

Delayed threshold response of a rodent population to human-induced landscape change

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Abstract Theory predicts that due to their resilience, ecosystems and populations are expected to respond to environmental changes not gradually, but in a nonlinear way with sudden abrupt shifts. However, it is not easy to observe and predict the state-and-transition dynamics in the real world because of time lags between exogenous perturbations and species response. Based on yearly surveys, during 21 years (1994–2014), we have studied population dynamics of a desert rodent (the midday gerbil, *Meriones meridianus*) in the rangelands of southern Russia under landscape change from desert to steppe caused by the drastic reduction of livestock after the collapse of the USSR in the early 1990s. The population of *M. meridianus* has remained robust to landscape change from desert to steppe for over 10 years, but then has suddenly dropped down and has not recovered since. The step transition from the high- to low-abundance density-regulated equilibrium was accompanied by an abrupt increase in the spatio-temporal population variability, which may indicate the loss of population resilience. We explain inertia in species response to landscape change and an abrupt regime shift in population dynamics by species-specific ecology and life-history combined with habitat fragmentation that had reached a certain critical threshold level by the early 2000s. This is a rare well-documented demonstration of a delayed threshold response of

a wild unexploited mammal population to human-induced environmental change, which may shed light on the mechanisms of population resilience and underlying causes of threshold population dynamics in a changing world.

Keywords Population dynamics · Population resilience · Environmental change · Gerbils

Introduction

Resilience is a fundamental feature of all natural systems, allowing them to stay in the same regime or state and to retain the same structure, function, and feedbacks in spite of exogenous disturbances (Carpenter and Folke 2006; Suding and Hobbs 2008). Theory predicts that, due to their resilience, ecosystems and populations should exhibit nonlinear state-and-transition dynamics under environmental change with delayed sudden threshold responses to human–nature interactions (Carpenter and Folke 2006; Liu et al. 2007; Suding and Hobbs 2008; Mori et al. 2013). Threshold response leads to a regime shift between alternate steady states of biological systems when a trigger switches the negative feedbacks from one attractor to another, or can even result in the system collapse (Scheffer et al. 2001; Carpenter and Folke 2006; Suding and Hobbs 2008; Dai et al. 2012). However, it is not easy to observe and predict the state-and-transition population dynamics in the real world because of time lags between the environmental change and species response. Thus, there is a strong need for high-quality field data based on long-term observations of natural populations in a changing environment, which are lacking (Coulson et al. 2001; Scheffer et al. 2001; Carpenter and Folke 2006; Liu et al. 2007; Dai et al. 2012).

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Political and socio-economic perturbations can cause ecosystem transformation and affect plant and animal populations (Hölzel et al. 2002; Liu et al. 2007; Werger and van Staalduinen 2012; Bragina et al. 2015), providing a rare opportunity to study and understand fundamental aspects of ecosystem and population dynamics and their resilience in the face of unpredictable environmental change (Scheffer et al. 2001; Carpenter and Folke 2006; Suding and Hobbs 2008; Wiens and Hobbs 2015).

Rangelands are good model ecosystems to study ecological resilience and state-and-transition dynamics, because they are very sensitive to human impact and can exhibit abrupt regime shifts in response to human-induced environmental change in time or space (Lockwood and Lockwood 1993; Sasaki et al. 2008). In the semi-arid zone of the southern Russia (in particular, in the Republic of Kalmykia), the establishment of the Soviet power in the 1920s was followed by a transition from the traditional nomadic seasonal pasturing practice to unregulated intensive settled livestock ranching on year-round stationary pastures (Saiko and Zonn 1997; Smelansky and Tishkov 2012). The overgrazing by sheep and cattle triggered desertification process in the 1960s, and by the 1980s, the originally semi-desert landscape had turned into sandy desert with a sparse cover of short annual grasses and forbs and vast areas of non-stabilized sands (Saiko and Zonn 1997; Shilova et al. 2000). In parallel, the populations of desert rodents (e.g., gerbils) had been increasing in numbers and range (Varshavsky et al. 1991). Models predicted that the desertification would spread over the entire area of Kalmykia by the beginning of the twenty-first century (Vinogradov 1995).

However, the breakdown of the Soviet state farm system after the collapse of the USSR in the late 1980s and early 1990s resulted in a rapid and drastic reduction of the livestock population. In turn, this triggered a rapid recovery of degraded Kalmykian rangelands and favored the expansion of steppe perennial grasses and herbs, and by the mid-1990s, the desert in Kalmykia had turned into a steppe-like landscape (Neronov et al. 1997; Shilova et al. 2000; Hölzel et al. 2002; Dubinin et al. 2011; Smelansky and Tishkov 2012). Such rapid human-induced large-scale landscape transformation provided an excellent opportunity to study species-specific responses to environmental change, as well as factors and mechanisms responsible for population resilience and delayed effects.

In earlier studies, we have shown that steppe expansion in Kalmykia produced a quick and predictable response in some rodent species (Shilova et al. 2000). For example, a rapid and substantial decline and range contraction in response to vegetation recovery was observed in the early 1990s in the open-dwelling ground squirrel, *Spermophilus pygmaeus* (Shilova et al. 2011), which prefers

lowly productive desert and semi-desert habitats (Rogovin 2007). In contrast, mesophilic folivorous species, such as the tamarisk gerbil, *Meriones tamariscinus*, and the social vole, *Microtus socialis*, which were rare during the “desert period” and occurred only in habitats associated with the irrigation system, increased in numbers and expanded their ranges to the rapidly recovering pastures (Shilova et al. 2000). However, contrary to expectations, a desert-dwelling psammophilous *Meriones meridianus* (the midday gerbil) showed no evident response to the contraction of the desert in short-term perspective (Shilova et al. 2000), suggesting that the time series was too short to detect a delayed species response to environmental change and that different species from local community vary in sensitivity and resilience to landscape transformation. Species response diversity is crucial for the resilience of an ecosystem as a whole, but so far is poorly understood (Elmqvist et al. 2003; Mori et al. 2013). In this study, we focus on the long-term effects of environmental change on populations of *M. meridianus* and report a delayed threshold population response of this species to human-induced landscape transformation from desert to steppe in Kalmykia, based on 21-year observations (1994–2014). We relate the observed threshold effect to the species ecology, life history and social organization and show that long-term observations are crucial for detecting non-linear patterns and regime shifts in population dynamics and understanding species-specific causes of population resilience to environmental change.

Materials and methods

Study area

The study was carried out in southern Kalmykia, Russia (45°29'N, 45°26'E). The climate is continental with hot dry summers (40–45 °C in July) and cold winters (–20 to –30 °C in January) typically with no snow cover. The area is located in the transition zone from dry steppe to desert and was used as winter pastures for sheep and cattle before the Soviet times and as year-round pastures thereafter (Saiko and Zonn 1997; Hölzel et al. 2002; Smelansky and Tishkov 2012). The vegetation is represented by annuals, perennial grasses and herbs, forbs, and scattered shrubs on sandy or loamy soils (Neronov et al. 1997).

Study object

Meriones meridianus is a small-sized (40–50 g) desert-dwelling rodent inhabiting arid zones from the Northern Caucasus and eastern Iran to Central Asia, Northern Afghanistan, Mongolia and Northern China. It is mainly granivorous and psammophilous and occur in open desert

habitats on stabilized, semi-stabilized or non-stabilized sands (Shenbrot et al. 1999; Rogovin 2007). In Kalmykia, midday gerbils prefer desert habitats disturbed by grazing and apparently avoid steppe tall-grass communities at advanced stages of recovering succession (Neronov et al. 1997; Isaev and Shilova 2000; Shilova et al. 2000; Rogovin 2007).

Data collection

Yearly, from 1994 through 2014, in autumn, in the end of the reproductive period (late Sept–early Oct), we captured gerbils on 6 permanent 250- ($n = 2$) and 500-m ($n = 4$) transects of 50 and 100 snap-traps, respectively, in a rangeland area of approximately 10 km². Three of them were situated in sandy plains and the other three in sandy hills, the most preferred habitats by *M. meridianus*.

Traps were baited with bread soaked in sunflower oil in the late evening and checked in the early morning. Trapping sessions within each sampling location lasted for two consequent nights. In total, we captured 725 gerbils—on average 5.8 individuals per site each year. *M. meridianus* is not an endangered species and is treated as pest in Russia. Snap trapping is a traditional survey method for long-term studies of rodent populations and does not affect population dynamics (Christensen and Hörnfeldt 2003; Hörnfeldt 2004). The procedure of trapping has remained the same throughout the entire study period, and the data have been collected by the same collectors.

Data treatment and time-series analysis

We estimated the relative abundance of gerbils as the number of individuals trapped per 100 trap nights averaged for the 6 sampling sites. For the subsequent time-series

analysis, the relative abundance index, N_t , was ln-transformed. Population growth rate, r , was calculated as $r = \ln(N_t/N_{t-1})$, where N_t is the abundance in the current year, and N_{t-1} is the abundance in the previous year.

To assess the variability of the spatial distribution of gerbils, we used the coefficient of variation (CV) and skewness of abundance distribution of gerbils across sampling sites (untransformed data) (Carpenter and Brock 2006; Drake and Griffen 2010; Dai et al. 2012). Increased variability is an early warning signal of ecological regime shifts or collapse (Carpenter and Brock 2006; Carpenter and Folke 2006; Drake and Griffen 2010; Dai et al. 2012). We used the standard deviations (SD) of the multi-year population metrics (Table 1) to measure population variability across the time series as suggested by Fraterrigo and Rusak (2008).

Since time-series data exhibited step-trend (see below), we splitted the whole series into two sequences (periods, 1994–2002 and 2003–2014), and analyzed the entire series as well as the two periods separately (Turchin 2003; Berryman and Lima 2006). All data conformed to requirements of normal distribution (Shapiro–Wilk’s test, $P > 0.2$). To analyze the variation in population parameters across years and between the two periods of the time series, we used t tests and analyses of covariance (ANCOVA) with the period of the time series as a factor and the year as a covariate. To compare population variability between the two periods of the time series, we used Levene’s test for homogeneity of variance of population parameters as suggested by Fraterrigo and Rusak (2008).

To describe the endogenous population dynamics and to analyze density-dependent effects on population abundance and growth, we detrended ln-transformed data using linear trend to remove the effects of exogenous factors. We used a partial correlation of r_t on $\ln N_{t-d}$ (Gompertz model),

Table 1 Population parameters for the two periods of the time-series data for *M. meridianus*

Parameters	Period	Mean (n)	SD	CI 95 %	t value, P	ANCOVA results $F_{1,18}$, P	
						Effect of the period (factor)	Effect of the year (covariate)
$\ln N$	1994–2002	1.97 (9)	0.33	1.70–2.21	5.62, 0.00002	5.89, 0.03	0.22, 0.65
	2003–2014	0.57 (12)	0.68	0.13–1.00			
r	1994–2002	0.02 (8)	0.50	−0.40–0.43	0.43, 0.7	0.72 ^b , 0.4	0.54 ^b , 0.47
	2003–2014	−0.14 (12)	0.95	−0.44–0.46			
CV ^a _{sites}	1994–2002	77.4 (9)	24.7	58.4–96.3	−5.25, 0.00005	6.63, 0.02	0.004, 0.95
	2003–2014	144.3 (12)	31.6	124.2–164.3			
Skewness ^a _{sites}	1994–2002	0.28 (9)	0.61	−0.19–0.75	−3.84, 0.001	4.38, 0.05	0.04, 0.84
	2003–2014	1.31 (12)	0.60	0.93–1.69			

^a Untransformed data for abundance distribution across the six sampling sites

^b df 1,17

where d is the effect order (time lag in years for feedback response), as well as second-order autoregressive models for detrended ln-transformed data for the entire (not-split) time series to assess direct (first order) and delayed density effects (Forchhammer et al. 1998; Turchin 2003; Ims et al. 2008). Second-order log-linear models were applied to parsimoniously describe the population dynamics for many species and various ecological conditions (Ims et al. 2008). For the autoregressive model, second-order differencing data transformation was applied (Turchin 2003).

Results

The population dynamics of the midday gerbil exhibited a decreasing not-stationary step trend with a transition from the high- to low-abundance state (Fig. 1a). The population growth rate showed no trend over the entire time series

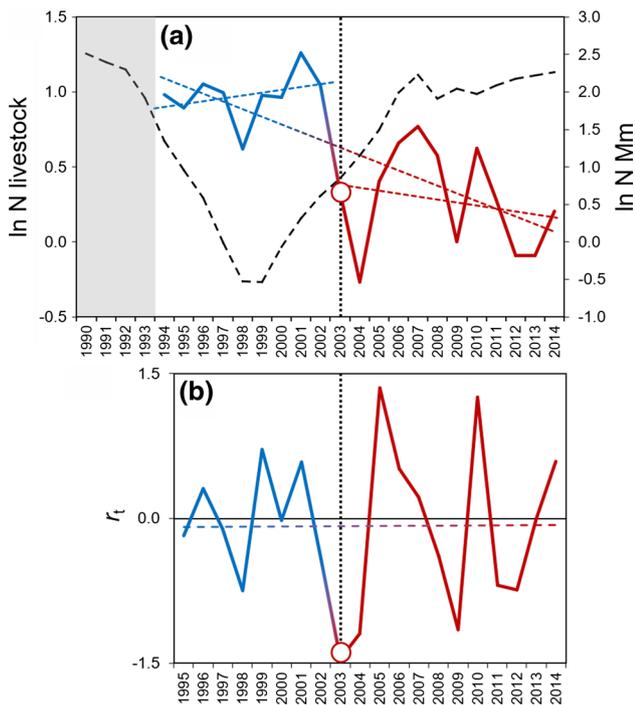


Fig. 1 Population dynamics of *M. meridianus* in Kalmykia. The dotted vertical line separates the entire time series (solid curve) into the periods before and after the population crash (the transition point) in 2003 (empty circle). **a** Time-series data (ln-transformed) for *M. meridianus* abundance (N individuals captured per 100 trap nights; averaged data for the 6 sampling sites) and livestock (dashed curve, millions heads; the Federal State Statistic Services: <http://www.gks.ru/dbscripts/cbsd/dbinet.cgi?pl=1416006>). Dashed lines show trends for the entire time series and for the pre- and post-crash periods separately. The shadowed area indicates the period before the beginning of the yearly surveys. **b** Time series for *M. meridianus* population growth rate, $r_t = \ln(N_t/N_{t-1})$. See also Table 1

($P = 0.98$), fluctuating around the equilibrium ($r = 0$) (Fig. 1b). Before and after transition point, the population showed strong fluctuations in abundance with no obvious trends within separated time series ($P > 0.4$), whereas the downward trend for the entire time series was highly significant ($r^2 = 0.51$, $F_{1,19} = 19.6$, $P < 0.001$; Fig. 1a). During the first period (1994–2002), *M. meridianus* stayed in the same regime of high abundance in spite of rapidly decreasing livestock population. Moreover, after drastic decline in 1998, *M. meridianus* had quickly recovered and remained highly abundant until the population crash in 2003, when a critical transition to the low-abundance regime occurred (that is, more than 10 years after the beginning of livestock decline and steppe expansion). The population has not recovered since and stays in the low-abundance regime in spite of rapidly increasing livestock population (Fig. 1a).

The population trajectory within the state space (Fig. 2) demonstrates a jump-like transition from one attractor around the equilibrium at high abundance (higher carrying capacity) to another at low abundance (lower carrying capacity) with a negative first-order density-dependent effect on the population growth rate, r_t , in both periods

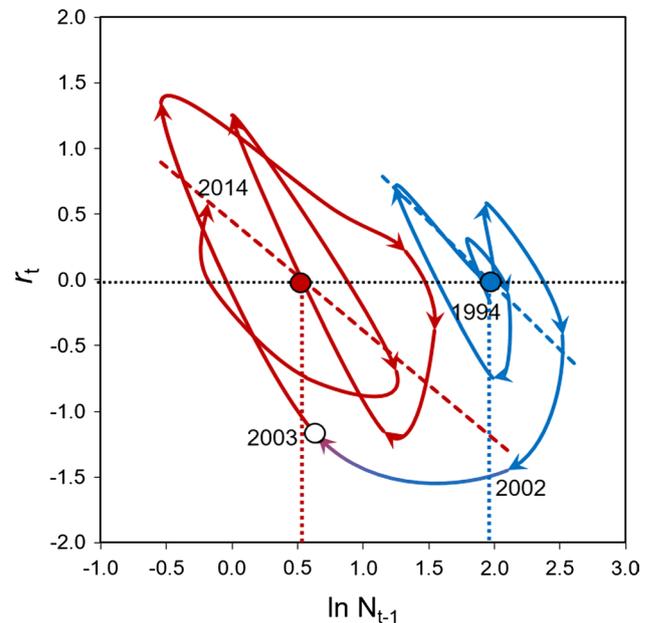


Fig. 2 Population trajectory (1994–2014) within the state space of the population abundance, $\ln N_{t-1}$, and the population growth rate, r_t . The empty circle indicates the transition from one equilibrium (blue circle, 1994–2002 period) to another (red circle, 2003–2014 period) in 2003. The horizontal dotted line shows the equilibrium level of $r_t = 0$. Vertical dotted lines correspond to multi-year mean abundances (carrying capacities) for the two periods. The negative relationship between $\ln N_{t-1}$ and r_t was significant for 2003–2014 ($r^2 = 0.50$, $F_{1,10} = 10.1$, $P < 0.01$) and borderline significant for 1994–2002 ($r^2 = 0.48$, $F_{1,6} = 5.6$, $P = 0.056$). Arrows show the direction of the time series (colour figure online)

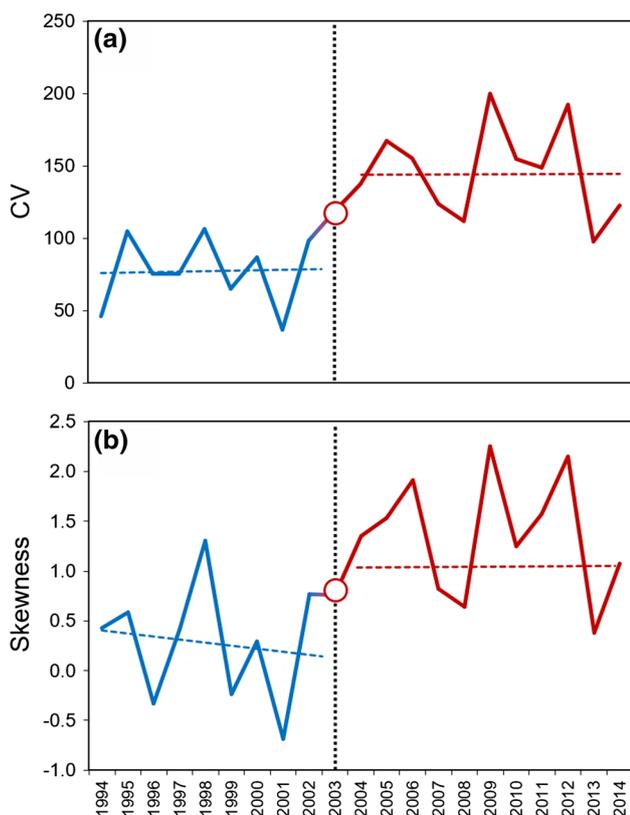


Fig. 3 Dynamics of *M. meridianus* abundance distribution across habitats. **a** Coefficient of variation and **b** skewness of abundance distribution (N individuals captured per 100 trap nights, untransformed) across the 6 sampling sites. See also Table 1

(ANCOVA, $\ln N_{t-1}$ effect: $F_{1,17} = 16.9$, partial $\eta^2 = 0.50$, $P = 0.0007$; period effect: $F_{1,17} = 10.6$, partial $\eta^2 = 0.38$, $P = 0.005$).

Similarly, a step transition in the time series was revealed for CV and skewness of the abundance distribution across the six sampling sites (Fig. 3a, b). No trends were observed for either parameter within separated time series before and after transition point in 2003 ($P = 0.72$ – 1.00). The distribution of gerbils across sites was significantly more variable

and skewed in the post-crash period (Table 1). Subsequent to the crash in 2003, gerbils have never been observed at two of the six sites (both situated in sandy plains, not in hills), while before the crash, they had been continuously recorded at all six sites.

All population parameters except r differed significantly between the pre- and post-crash periods, but did not vary between years when controlled for the effect of the period in the general linear model (ANCOVA, Table 1). Population variability (as indicated by standard deviations) in terms of abundance, growth rate, and distribution across sites was higher during the post-crash period. Levene’s test indicated significant increase in variances of population abundance and growth rate after the high-to-low transition ($F_{1,19} = 6.44$, $P = 0.02$ and $F_{1,18} = 5.12$, $P = 0.04$, respectively).

The partial correlation and autoregressive model revealed both direct and delayed second-order density dependence effects (Table 2). The population growth rate was negatively correlated with the abundance in the previous year and the year before that. Consequently, the population abundance exhibited significant negative delayed density dependence with the time lag of 2 years.

Discussion

Since *M. meridianus* is a desert-dwelling psammophilous species and desertification in Kalmykia in the 1960s–1980s favored its quick expansion and increase in abundance (Varshavsky et al. 1991), one could expect its population and range to decrease substantially along with the contraction of desert and expansion of steppe after the drastic reduction of the livestock population in the early 1990s. However, unlike other rodent species from local community, and contrary to expectations, the population of *M. meridianus* has remained robust to the landscape change from desert to steppe for a decade despite the decreasing grazing impact and ongoing process of steppe expansion, and only then experienced a step-like transition from the high- to

Table 2 Direct and delayed density-dependent effects in population dynamics of the midday gerbil in Kalmykia

Density dependence tests ^a							
Effect order, d^c	Partial correlation of r_t on $\ln N_{t-d}$			AR(2) ^b , $n = 16$			
	Coefficient	$t(n)$	P	Parameter	Coefficient \pm SE	t	P
1	–0.61	–3.28 (18)	0.004	β_1	0.45 ± 0.19	2.33	0.030
2	–0.53	–2.56 (17)	0.020	β_2	$–0.70 \pm 0.19$	–3.63	0.002

^a In-transformed detrended data

^b The second-order autoregressive model $X_t = \beta_0 + \beta_1 X_{t-1} + \beta_2 X_{t-2} + \varepsilon(1)$, where X_t is the logarithm of population abundance in year t , β_1 and β_2 are the parameters of the direct and the delayed density dependence, respectively, β_0 is a constant, and ε is a noise term (Ims et al. 2008)

^c Time lag (years) for feedback response

low-abundance density-regulated state. This indicates a delayed threshold population response to environmental change with a regime shift and switch of a negative density-dependent feedback from one domain of attraction to another (Suding and Hobbs 2008). The inertia in response to changing environment shown by *M. meridianus* can be attributed to its ecological generalism, habitat opportunism and relatively high niche breadth (Shenbrot et al. 1999; Fu et al. 2004; Rogovin 2007), which could enhance a species resilience to exogenous perturbations (and, in particular, to habitat fragmentation; Ewers and Didham 2006) allowing to cope with changing environment and stay in the same regime until the critical level of change had been reached.

One could suggest that the observed sudden and (so far) irreversible shift in the population state is not a delayed threshold response of a resilient population to the landscape change, but rather a result of a shift in some other exogenous limiting factor that caused immediate dramatic decline in abundance in 2003 (Berryman 1999). One of the exogenous factors that could potentially cause an abrupt shift in the population state is grassland fires, which had never been observed here during the “desert period”, but became common during the “steppe period” (Dubinin et al. 2011). Burnings stimulated further tall-grass expansion, thus contributing to the landscape change, but produced only slight and short-term direct effects on the midday gerbil population. Specifically, fires caused some redistribution of gerbils in space (in favor of burned patches) and some decrease in fecundity (Shilova et al. 2007). Moreover, within the study area, fires occurred once in 2–3 years during the period from 1995 to 2006, i.e., long before and some after the tipping point (2003) in the midday gerbil population dynamics, and have not been recorded since. So, it is very unlikely that fires had caused an immediate abrupt shift in gerbil population dynamics.

Also, an epizootic process could cause drastic and long-lasting population decline. *M. meridianus* is a main natural carrier of plague in Kalmykia; however, epizootics have not been recorded here by the State Plague Control Service since 1991 (Popov et al. 2011). Finally, no drastic changes in the land-use practice were observed during the study period. This area is traditionally used as pastures for sheep and cattle only, and no ploughing or any other agricultural activity occurs here. New practice of tall-grass mowing was invented in restricted areas in 2007, after the tipping point in population dynamics, and it is unlikely that local mowing could significantly affect the midday gerbil population. Thus, since no other exogenous factor, except grazing impact, varied strongly across the time series or changed drastically at the transition point of gerbil population dynamics, and the decline in livestock numbers in early 1990s is recognized as the major driver of the landscape

transformation in Kalmykia in the mid-1990s (Neronov et al. 1997; Shilova et al. 2000, 2007; Hölzel et al. 2002; Dubinin et al. 2011; Smelansky and Tishkov 2012), the observed abrupt shift in population regime can be explained by the delayed threshold response of a resilient population of a generalist species to the landscape change.

Threshold responses of resilient biological systems to exogenous disturbances are predicted by theory; however, so far, they were rarely observed in natural populations. Threshold population dynamics with abrupt regime shifts caused by the Allee effect (i.e., the negative per capita growth rate at low densities because of difficulties in finding mates; Allee et al. 1949) and loss of population resilience before the tipping point were observed in the laboratory populations of yeast cells under experimentally manipulated density and environment (Dai et al. 2012). Sudden collapse of the critically endangered saiga antelope population (*Saiga tatarica tatarica*) was observed in Kalmykia and was attributed to the low proportion of adult males that dropped below critical level as a result of selective poaching (Milner-Gulland et al. 2003). Interestingly, the collapse of saiga occurred in 2001, 10 years after the disintegration of the state wildlife protection services and the beginning of heavy poaching and overexploitation. Abrupt regime shifts were shown for overexploited fish populations (Frank et al. 2011). Sudden transition from cycling to non-cycling population regime in the mid-1980s was reported for some voles (*Myodes* and *Microtus*) in boreal zone and was explained by climate change (Hörnfeldt 2004; Ims et al. 2008). Variation of grazing impact along spatial gradient was found to produce threshold response in vegetation on Mongolian pastures (Sasaki et al. 2008). To our knowledge, findings of this study represent the first well-documented demonstration of a delayed threshold response of a wild unexploited mammal population to landscape change caused by socio-economic perturbations.

The presence and value of critical thresholds are influenced by landscape dynamic patterns and species characteristics, and habitat fragmentation is one of the possible causes of nonlinear species dynamics with delayed threshold responses (Swift and Hannon 2010). The ultimate reason for the delayed step-like transition from the high- to low-abundance population regime in *M. meridianus* could be the transformation and fragmentation of the desert habitats caused by the rangeland recovery and steppe expansion that had approached a certain critical threshold level by the early 2000s. Prior to that (in 1998), the population was able to recover after the drastic decline, while the crash of 2003, presumably caused by some exogenous factor (e.g., severe winter), overwhelmed population resilience and pushed it across the unstable point to a new low-abundance equilibrium, where it stays until now showing no response to

increasing grazing. The increased spatio-temporal population variability observed during the current post-crash period may indicate the loss of resilience and suggests lower resistance to further environmental perturbations (Carpenter and Brock 2006; Drake and Griffen 2010; Dai et al. 2012).

Proximately, the step transition to low abundance regime could be a result of the increased mortality and the strong Allee effect in fragmented landscape. Metapopulation model that incorporates both habitat loss and Allee effects shows that Allee effects can lead to critical threshold relationships between population size and habitat amount (Amarasekare 1998; Swift and Hannon 2010). The loss of habitat connectivity can restrict dispersal and/or increase the mortality during dispersal and the risk of not finding a mate (Hanski 1999; Banks et al. 2007). We suggest that when desert habitat fragmentation had reached critical level, increased mortality during dispersal combined with the Allee effect did not allow a population to recover after the crash in 2003 and it switched to an alternative low-abundance state. Similar threshold response attributed to the strong Allee effect was found in the laboratory populations of yeast cells, where populations with higher mortality, unlike those with lower mortality, were not able to recover after exogenous shock and switched to a new low-abundance regime or went extinct (Dai et al. 2012).

Species patterns of reproduction, dispersal and social system can also contribute to threshold responses to habitat fragmentation and should be taken into account when analyzing and predicting population dynamics under landscape change (Banks et al. 2007; Swift and Hannon 2010). Midday gerbils live solitary, exhibit strong site fidelity and show no density-dependent reproduction either in laboratory, or in the wild (Gol'tsman et al. 1994; Shilova and Tchabovsky 2009). Low density in a patch does not stimulate reproduction of survivors or immigration even from the closest inhabited patches with high density. As a result, midday gerbils exhibit slow population recovery pattern after the population crash, and vacant habitats are recolonized only by dispersing young (Shilova and Orlov 2004; Shilova and Tchabovsky 2009). Thus, strong site fidelity and density-independent reproduction combined with habitat connectivity loss and the Allee effect could be responsible for threshold population response and regime shift after the population crash in fragmented landscape.

Our results suggest that the predictability of the response of the mammalian populations, and indeed of the whole ecosystem to a human-induced diverse and complex landscape dynamics may be limited. More generally, our findings show that long-term observational studies are crucial for understanding species-specific mechanisms of population resilience and underlying causes of threshold population dynamics in a changing world.

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Author contribution statement A.T., L.S., and N.O. collected and treated the data. A.T., E.S and I.K. performed the analysis. A.T. and E.S. wrote the paper. All authors contributed substantially to revisions of the draft paper.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

References

- Allee WC, Park O, Emerson AE, Park T, Schmidt KP (1949) Principles of animal ecology. Saunders, Philadelphia
- Amarasekare P (1998) Allee effects in metapopulation dynamics. *Am Nat* 152:298–302
- Banks SC, Piggott MP, Stow AJ, Taylor AC (2007) Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions. *Can J Zool* 85:1065–1079. doi:10.1139/Z07-094
- Berryman A (1999) Principles of population dynamics and their application. Stanley Thornes, Cheltenham
- Berryman A, Lima M (2006) Deciphering the effects of climate on animal populations: diagnostic analysis provides new interpretation of Soay sheep dynamics. *Am Nat* 168:784–795. doi:10.1086/508670
- Bragina EV, Ives AR, Pidgeon AM, Kuemmerle T, Baskin LM, Gubar YP, Piquer-Rodríguez M, Keuler NS, Petrosyan VG, Radeloff VC (2015) Rapid declines of large mammal populations after the collapse of the Soviet Union. *Conserv Biol* 29:844–853. doi:10.1111/cobi.12450
- Carpenter SR, Brock WA (2006) Rising variance: a leading indicator of ecological transition. *Ecol Lett* 9:311–318. doi:10.1111/j.1461-0248.2005.00877.x
- Carpenter SR, Folke C (2006) Ecology for transformation. *Trends Ecol Evol* 21:309–315. doi:10.1016/j.tree.2006.02.007
- Christensen P, Hörnfeldt B (2003) Long-term decline of vole populations in northern Sweden: a test of the destructive sampling hypothesis. *J Mammal* 84:1292–1299. doi:10.1644/BBa-014
- Coulson T, Mace GM, Hudson E, Possingham H (2001) The use and abuse of population viability analysis. *Trends Ecol Evol* 16:219–221. doi:10.1016/S0169-5347(01)02137-1
- Dai L, Vorselen D, Korolev KS, Gore J (2012) Generic indicators for loss of resilience before a tipping point leading to population collapse. *Science* 336:1175–1177. doi:10.1126/science.1219805
- Drake JM, Griffen BD (2010) Early warning signals of extinction in deteriorating environments. *Nature* 467:456–459. doi:10.1038/nature09389

- Dubinin M, Luschekina A, Radeloff V (2011) Climate, livestock, and vegetation: what drives fire increase in the arid ecosystems of Southern Russia? *Ecosystems* 14:547–562. doi:[10.1007/s10021-011-9427-9](https://doi.org/10.1007/s10021-011-9427-9)
- Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. *Front Ecol Environ* 1:488–494. doi:[10.1890/1540-9295\(2003\)001\[0488:RDECAR\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001[0488:RDECAR]2.0.CO;2)
- Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biol Rev* 81:117–142. doi:[10.1017/S1464793105006949](https://doi.org/10.1017/S1464793105006949)
- Forchhammer MC, Stenseth NC, Post E, Landvatn R (1998) Population dynamics of Norwegian red deer: density-dependence and climatic variation. *Proc R Soc B* 265:341–350. doi:[10.1098/rspb.1998.0301](https://doi.org/10.1098/rspb.1998.0301)
- Frank KT, Petrie B, Fisher JA, Leggett WC (2011) Transient dynamics of an altered large marine ecosystem. *Nature* 477:86–89. doi:[10.1038/nature10285](https://doi.org/10.1038/nature10285)
- Fraterrigo JM, Rusak JA (2008) Disturbance-driven changes in the variability of ecological patterns and processes. *Ecol Lett* 11:756–770. doi:[10.1111/j.1461-0248.2008.01191.x](https://doi.org/10.1111/j.1461-0248.2008.01191.x)
- Fu H, Wu X, Yang Z, Xu Y (2004) Comparing of niche for rodent species in Alashan desert region of Inner Mongolia. *Chin J Zool* 39:27–34
- Gol'tsman ME, Popov SV, Chabovskii AV, Borisova NG (1994) The sociality syndrome. A comparative study of the behavior of gerbils. *Zh Obshch Biol* 55:49–69 (in Russian)
- Hanski I (1999) Metapopulation ecology. Oxford University Press, New York
- Hölzel N, Haub C, Ingelfinger MP, Otte A, Pilipenko VN (2002) The return of the steppe large-scale restoration of degraded land in southern Russia during the post-Soviet era. *J Nat Conserv* 10:75–85. doi:[10.1078/1617-1381-00009](https://doi.org/10.1078/1617-1381-00009)
- Hörnfeldt B (2004) Long-term decline in numbers of cyclic voles in boreal Sweden: analysis and presentation of hypotheses. *Oikos* 107:376–392. doi:[10.1111/j.0030-1299.2004.13348.x](https://doi.org/10.1111/j.0030-1299.2004.13348.x)
- Ims RA, Henden JA, Killengreen ST (2008) Collapsing population cycles. *Trends Ecol Evol* 23:79–86. doi:[10.1016/j.tree.2007.10.010](https://doi.org/10.1016/j.tree.2007.10.010)
- Isaev SI, Shilova SA (2000) Biotopic distribution of the midday (*Meriones meridianus*) and tamarisk (*M. tamariscinus*) gerbils (Rodentia, Gerbillinae) in the Southern Kalmyk Republic. *Izv Akad Nauk Ser Biol* 1:94–99 (in Russian)
- Liu J, Dietz T, Carpenter SR, Alberti M, Folke C, Moran E, Pell AN, Deadman P, Kratz T, Lubchenco J, Ostrom E, Ouyang Z, Provencher W, Redman CL, Schneider SH, Taylor WW (2007) Complexity of coupled human and natural systems. *Science* 317:1513–1516. doi:[10.1126/science.1144004](https://doi.org/10.1126/science.1144004)
- Lockwood JA, Lockwood DR (1993) Catastrophe theory: a unified paradigm for rangeland ecosystem dynamics. *J Range Manag* 46:282–288. doi:[10.2307/4002459](https://doi.org/10.2307/4002459)
- Milner-Gulland EJ, Bukreeva OM, Coulson T, Lushchekina AA, Kholodova MV, Bekenov AB, Grachev IA (2003) Conservation: reproductive collapse in saiga antelope harems. *Nature* 422:135. doi:[10.1038/422135a](https://doi.org/10.1038/422135a)
- Mori AS, Furukawa T, Sasaki T (2013) Response diversity determines the resilience of ecosystems to environmental change. *Biol Rev* 88:349–364. doi:[10.1111/brv.12004](https://doi.org/10.1111/brv.12004)
- Neronov VV, Tchabovskii AV, Aleksandrov DY, Kasatkin MV (1997) Spatial distribution of rodents under conditions of anthropogenic dynamics of vegetation in the South of Kalmykia. *Russ J Ecol* 28:328–334
- Popov NV, Bezsmertny VE, Matrosov AN, Nemchenko LS, Verzhutsky DB, Maletskaya OV, Udovikov AI, Kuznetsov AA, Knyazeva TV, Shilova LD, Gorshenko VV, Popov VP, Toporkov VP, Toporkov AV, Kutyrav VV (2011) Epizootic activity of plague natural foci in the Russian Federation in 2010 and prognosis for 2011. *Probl Osobo Opasn Infek* 1:1–37 (in Russian)
- Rogovin KA (2007) Steppe expansion and changes in the structure of the rodent community in north-western Caspian region (Republic of Kalmykia, RF). *Acta Zool Sin* 53:29–43
- Saiko T, Zonn I (1997) Europe's first desert. In: Werger MJA, van Staaldunin MA (eds) Eurasian steppes. Ecological problems and livelihoods in a changing world. Springer, Netherlands, pp 141–144
- Sasaki T, Okayasu T, Jamsran U, Takeuchi K (2008) Threshold changes in vegetation along a grazing gradient in Mongolian rangelands. *J Ecol* 96:145–154. doi:[10.1111/j.1365-2745.2007.01315.x](https://doi.org/10.1111/j.1365-2745.2007.01315.x)
- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413:591–596. doi:[10.1038/35098000](https://doi.org/10.1038/35098000)
- Shenbrot GI, Krasnov B, Rogovin KA (1999) Spatial ecology of desert rodent communities. Springer, Berlin
- Shilova SA, Orlov DP (2004) Certain behavioral traits of small mammals in abnormal social environment. *Biol Bull Russ Acad Sci* 31:358–366. doi:[10.1023/B:BIBU.0000036940.94275.7f](https://doi.org/10.1023/B:BIBU.0000036940.94275.7f)
- Shilova SA, Tchabovskii AV (2009) Population response of rodents to control with rodenticides. *Curr Zool* 55:81–91
- Shilova SA, Chabovskii AV, Isaev SI, Neronov VV (2000) Dynamics of rodent community and populations in Kalmyk semideserts under decreasing pasture load and increasing humidity. *Izv Akad Nauk Ser Biol* 3:332–344 (in Russian)
- Shilova SA, Neronov VV, Kasatkin MV, Savinetskaya LE, Tchabovskii AV (2007) Fires at the current stage of evolution of semi-desert in southern Russia: the influence on vegetation and rodent populations. *Usp Sovr Biol* 127:372–386 (in Russian)
- Shilova SA, Savinetskaya LE, Neronov VV (2011) The 28-year abundance and biomass dynamics of the little ground squirrel (*Spermophilus pygmaeus* Pall., 1778) in the pasture ecosystems of Kalmykia. *Arid Ecosyst* 1:177–183. doi:[10.1134/S2079096111030103](https://doi.org/10.1134/S2079096111030103)
- Smelansky IE, Tishkov AA (2012) The steppe biome in Russia: ecosystem services, conservation status, and actual challenges. In: Werger MJA, van Staaldunin MA (eds) Eurasian steppes. Ecological problems and livelihoods in a changing world. Springer, Netherlands, pp 45–101
- Suding KN, Hobbs RJ (2008) Threshold models in restoration and conservation: a developing framework. *Trends Ecol Evol* 24:271–279. doi:[10.1016/j.tree.2008.11.012](https://doi.org/10.1016/j.tree.2008.11.012)
- Swift TL, Hannon SJ (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. *Biol Rev* 85:35–53. doi:[10.1111/j.1469-185X.2009.00093.x](https://doi.org/10.1111/j.1469-185X.2009.00093.x)
- Turchin P (2003) Complex population dynamics: a theoretical/empirical synthesis (MPB-35). Princeton University Press, Princeton
- Varshavsky SN, Popov NV, Varshavsky BS, Shilov MN, Tikhomirov EL, Bugakov AA (1991) Modification of the species composition of rodents in the north-western region of the Caspian sea area under the effect of anthropogenic factors. *Zool Zh* 70:92–100 (in Russian)
- Vinogradov BV (1995) Forecasting dynamics of deflated sands of Black Lands, Kalmykia using aerial photography. In: Zonn IS, Neronov VM (eds) Biota and environment of Kalmykia. Korkis, Moscow, pp 259–268 (in Russian)
- Werger MJA, van Staaldunin MA (2012) Eurasian steppes. Ecological problems and livelihoods in a changing world. Springer, Netherlands
- Wiens JA, Hobbs RJ (2015) Integrating conservation and restoration in a changing world. *Bioscience* 65:302–312. doi:[10.1093/biosci/biu235](https://doi.org/10.1093/biosci/biu235)