Complex and nonlinear effects of weather and density on the demography of small herbivorous mammals

Lijun Chen[a], Guiming Wang[b], Xinrong Wan[a,*], Wei Liu[a]

[a]*State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang District, Beijing 100101, China*
[b]*Department of Wildlife, Fisheries and Aquaculture, Mail Stop 9690, Mississippi State University, Mississippi State, MS 39762, USA*

Abstract

Understanding differential and integral effects of weather and population density on vital rates (e.g., survival and recruitment rates) helps elucidate the ecological and demographic mechanisms underlying animal population dynamics. Nonlinear responses of vital rates to changes in weather conditions, such as precipitation, are important for predicting the effects of climate changes on small herbivorous mammals. We aimed to test the hypotheses: (1) that small herbivore populations increase from low to intermediate precipitation with improved habitat conditions and decline beyond the intermediate or optimum precipitation due to increased mortality in semi-arid grassland and (2) that increases in population size would result in stronger negative effects on recruitment than on survival of small mammals. We live-trapped a population of the Daurian pika (*Ochotona dauurica*), a small herbivorous mammal, in north central Inner Mongolia, China, biweekly between May and November from 2010 to 2012. We estimated the effects of temperature, precipitation, and population size on the survival probabilities and recruitment rates of *O. dauurica* using mark-recapture methods. Increases in temperature improved the recruitment but reduced the survival of *O. dauurica*, resulting in negative net effects on population growth rates. Increased precipitation initially resulted in positive effects and then had negative effects on population growth rates primarily through nonlinear effects on survival probabilities, supporting the optimum habitat hypothesis. Changes in population size had stronger effects on recruitment than on survival of *O. dauurica*, suggesting that density-dependent feedback to recruitment may be a primary regulatory mechanism of small mammal populations.

Zusammenfassung

Die unterschiedlichen und wesentlichen Einflüsse des Wetters und der Populationsdichte auf demographische Indikatoren (Überlebens- und Rekrutierungsraten) zu verstehen, hilft, die ökologischen und demographischen Mechanismen aufzuklären, die der Populationsdynamik von Tieren zugrunde liegen. Nichtlineare Reaktionen der demographischen Indikatoren auf Änderungen der Wetterbedingungen (z.B. Regenfälle) sind entscheidend, um die Auswirkungen von klimatischen Veränderungen auf herbivore Kleinsäuger vorherzusagen. Wir beabsichtigten die folgenden Hypothesen zu testen: (1) Die Populationen von herbivoren Kleinsäugern nehmen mit geringen bis mittleren Niederschlägen mit verbesserten Habitatbedingungen im semiariden Grasland zu, und nehmen jenseits der mittleren oder optimalen Niederschlagsmenge aufgrund gesteigerter Mortalität ab. (2) Zunahmen der Populationsgröße haben bei den Kleinsäugern stärker negative Effekte auf die Rekrutierung als auf das Überleben.

*Corresponding author. Tel.: +86 10 648 07106; fax: +86 10 648 07099.
E-mail address: wanxr@ioz.ac.cn (X. Wan).

Wir untersuchten eine Population des Daurischen Pfeifhasens (*Ochotona dauurica*), in der nordzentralen Inneren Mongolei (VR China) alle zwei Wochen zwischen Mai und November in 2010 bis 2012. Wir bestimmten die Einflüsse von Temperatur, Niederschlag und Populationsgröße auf die Überlebenswahrscheinlichkeit und die Rekrutierungsrate der Pfeifhasenpopulation mit Markierungs-Wiederfang-Methoden. Temperaturanstieg verbesserte die Rekrutierung und verringerte die Überlebensrate der Pfeifhasen mit negativem Gesamteffekt auf die Wachstumsrate der Population. Zunehmender Niederschlag hatte zunächst positive, dann aber negative Auswirkungen auf die Wachstumsrate, in erster Linie durch nichtlineare Effekte auf die Überlebenswahrscheinlichkeit. Dies stützt die Hypothese vom optimalen Habitat. Änderungen der Populationsgröße hatten stärkere Auswirkungen auf die Rekrutierung als auf das Überleben der Pfeifhasen, wodurch nahegelegt wird, dass dichteabhängige Rückkopplung auf die Rekrutierung ein grundlegender Regulationsmechanismus für Kleinsäugerpopulationen sein könnte.

Introduction

Intrinsic (e.g., population density) and extrinsic (e.g., weather, food, and predation) factors interact to influence the dynamics of animal populations (Karels & Boonstra, 2000; Lundberg et al., 2000). Intrinsic and extrinsic factors may act on different demographic processes (e.g., survival, reproduction, and recruitment) of animal populations in different directions and magnitudes. Therefore, the effects of weather and population density on vital rates (e.g., survival rate and recruitment rate) are critical to elucidate the ecological and demographic mechanisms underlying the dynamics of mammal populations in fluctuating environments (Coulson et al., 2005; Krebs, 2003).

Population variability includes demographic stochasticity and environmental stochasticity (Lande et al., 2003). Demographic stochasticity results from random or stochastic events such as death and birth, particularly in small populations. The vital rates of small mammals are responsive to changes in weather and population densities (Julliard et al., 1999; Morrison & Hik, 2007). Population growth rates of short-lived species are sensitive to environment-driven variability (i.e., environmental stochasticity) of all vital rates (Morris et al., 2008). As a result, populations of small mammals have strong environmental stochasticity (Wang et al., 2013). Additionally, the effects of weather or climate on the demography of small mammals may be nonlinear (Lima et al., 2002; Stenseth et al., 2002). For example, Brandt's voles (*Lasiopodomys brandtii*) in Inner Mongolia, China exhibit nonlinear responses to grass cover and grass height (Zhang et al., 2003). In semi-arid regions, plant biomass, grass height, and grass cover are positively related to precipitation. Understanding nonlinear responses of the vital rates and population growth rates to climate changes may help predict how small mammal populations may respond to future climate changes.

Density dependence is defined as decreases in population growth rate with increasing population densities or abundances. Population growth rates may be related to densities in the year $t-1$ (i.e., direct density dependence) or in the year $t-2$ (i.e., indirect density dependence; Lima et al., 2006).

Density dependence commonly occurs in small mammal populations (Wang et al., 2013). Direct density dependence may reduce reproduction and recruitment with increasing densities and subsequently stabilize population abundances of rodents (Ostfeld et al., 1993; Reed & Slade, 2008). Fecundity, juvenile survival, and immigration contribute to recruitment. Population growth rates of small mammals are more sensitive to changes in fecundity than to those in survival (Gaillard et al., 2005). Therefore, if density dependence serves as a regulatory mechanism of small mammal population dynamics, population density would have stronger effects on recruitment or fecundity than on survival (Morrison & Hik, 2007; Reed & Slade, 2008). However, the role of density dependence in population regulation is still debated in the ecological literature (Krebs, 2013).

The Daurian pika (*Ochotona dauurica*) is a small herbivorous mammal, widely distributed in the grassland on the Mongolian Plateau (Wang et al., 2003a). *O. dauurica* lives in social groups year round and reproduces from April to August (Chen et al., 2014; Zhong et al., 2008). Populations of *O. dauurica* often exhibit extreme fluctuations in population size, with frequent local extinctions during winter (Formozov, 1966). Increased precipitation enhances seasonal population growth rates of *O. dauurica* in Hexiten Qi (county), Inner Mongolia, China (Wang & Zhong, 2006); however, the habitat-occupancy probability of *O. dauurica* is inversely related to soil moisture content in Baiyinxile, Xilingol, Inner Mongolia (Wang et al., 2003b). The difference between the two studies may suggest optimal precipitation for the survival and population growth of *O. dauurica*, with low and high extremes being detrimental. The optimum habitat hypothesis states that the optimum habitat condition (e.g., weather condition) exists at the intermediate level and that population abundances increase from the low level to the optimum condition and decline beyond the optimum (Smith et al., 1999). However, to our knowledge, little is known about the effects of weather on the survival and recruitment of *O. dauurica*.

In this study, we estimated the directions and magnitudes of the effects of temperature, precipitation, and population size on the survival and recruitment of *O. dauurica* using

mark-recapture methods (Williams et al., 2001). In the grassland of central east Inner Mongolia, rain or storm water often drowns burrowing rodents such as Brandt's voles (X.R. Wan, personal observation). Therefore, we assume that the direct effects of precipitation on burrowing small mammals are appreciable. We tested for the nonlinear effects of precipitation on population growth rates and survival probabilities of *O. dauurica* as predicted by the optimum habitat hypothesis. We also tested the prediction that increases in population size have stronger negative effects on recruitment than on survival of *O. dauurica*. Moreover, American pikas (*Ochotona princeps*) and *O. dauurica* are distributed on high mountains and plateaus, respectively, and adapt to cold environments (Smith, 1978; Wang et al., 2003a). Warming and heat stress may lead to the local extirpation of *O. princeps* (Beever et al., 2010). We also hypothesize that increases in temperature would reduce survival and population growth rates of *O. dauurica*. The effects of changes in temperature and precipitation on *O. dauurica* populations may help understand the population dynamics of small herbivores in the arid and semi-arid grassland under future warming and increases in precipitation in northern latitudes (IPCC, 2007).

Materials and methods

Study area

We conducted the study at Naren Gacha (village), Abaga Qi in the typical steppe of Inner Mongolia, China (44°26′N, 114°58′E). The climate was semi-arid, with warm summers and cold winters. Monthly mean temperatures ranged from –22.9 to 23.6 °C. Mean annual total precipitation was about 250 mm, ranging from 135.0 to 267.2 mm. Snow cover lasted from mid- or late October to early May the following year. Vegetation on the study site mainly consisted of *Leymus chinense*, *Artemisia frigida*, *Allium polyrhizum*, *Salsola collina*, and *Chenopodium glaucum*, with *A. polyrhizum* as the dominant plant.

Live trapping of *O. dauurica*

We live-trapped *O. dauurica* biweekly on a 1.5 ha plot (140 m × 110 m) from 12 May 2010 to 28 October 2010, from 10 July 2011 to 11 October 2011, and from 20 May 2012 to 5 October 2012. The trapping plot initially had 33 pika burrow systems. *O. dauurica* remains active mainly under the snow cover during winter (G.M. Wang, personal observation). Therefore, we did not trap *O. dauurica* during winter to avoid trap mortality resulting from low temperatures.

We placed a wire-mesh live trap (28 × 13 × 10 cm) at each active burrow entrance in each burrow system. An active burrow entrance had piles of fresh, greenish feces and a runway connecting the entrance to another burrow entrance. We placed about 350–400 traps on the trapping plot each trapping week, with 8–12 traps per burrow system. We trapped during the diurnal or crepuscular activity periods. We set traps at 0500–0600 h, checked traps every 1 or 2 h until about 1100 h, and closed traps from 1100 to 1500 h to avoid trap mortality resulting from heat stress. Trapping resumed at 1600 h and continued until 1900 h. In May, September, and October, we set traps between 0630 and 0730 h and monitored them hourly until 1730 h. We tagged each captured pika with an ear tag with a unique identification (ID) number (S. Roestenburg, Herriman, UT, USA) at its first capture. We also sexed captured pikas and weighed them to the nearest 0.1 g with a portable electronic scale (Scout SE601F, Ohaus Corp., Parsippany, NJ, USA). We recorded ID number, trap location (i.e., burrow system ID), sex, and body mass for each capture and released the captured pika at the same trap station of capture immediately after handling. Our trapping and handling of *O. dauurica* was approved by the Institutional Animal Use and Care Committee (IACUC) of the Institute of Zoology, Chinese Academy of Sciences and Mississippi State University IACUC (protocol 11-031).

Analysis of survival and recruitment

We evaluated the effects of weather and density on weekly apparent survival (hereafter, survival) and recruitment of *O. dauurica* using Jolly–Seber (JS) models (Jolly, 1965; Seber, 1965). To reduce the number of possible combinations of temperature, precipitation, and density, for survival probability, recapture probability and recruitment rate in the JS model, we first used the Cormack–Jolly–Seber (CJS) model to determine covariates influencing pika survival and recapture probabilities (Cormack, 1964; Jolly, 1965; Seber, 1965). We tested the assumptions of no behavioral responses (i.e., not trap shy or happy) and no movement (i.e., no transient individuals) for the CJS models using tests 2CT and 3SR in the program UCARE (Choquet et al., 2009). We first built the CJS models including sex and time (i.e., trapping weeks) as categorical variables (hereafter, categorical-covariate models) to test whether survival and recapture probabilities of *O. dauurica* were sex-dependent and time-dependent. We built 16 categorical-covariate CJS models with all possible combinations of time and sex effects on the probabilities of survival and recapture (i.e., four different combinations for survival and four different combinations for recapture).

We used information-theoretic approaches to select the most parsimonious model to infer the effects of covariates (Burnham & Anderson, 2002). The model with the lowest value of Akaike information criterion corrected for small sample sizes (AICc) or highest Akaike weight (*w*) was the most parsimonious model, and models with ΔAICc value less than 2 were considered competing models, which are competitive with the best model with substantial empirical support by the data at hand (Burnham & Anderson, 2002). We estimated variance inflation factors, i.e., median c hat, using the most complex model with the time–sex interaction

on both survival and recapture probabilities (White & Burnham, 1999). If the value of median c hat was greater than 1.0, we used median c hat to scale the model deviances and compute quasi-Akaike information criterion corrected for small sample sizes (QAICc) in the model selection (White & Burnham, 1999).

If the effect of sex on survival or recapture probabilities was included in the most parsimonious model or competing categorical-covariate CJS models, we included sex effects in subsequent survival analyses. If survival probabilities varied over time in the most parsimonious or competing categorical-covariate model, we included density and weather variables as covariates of survival probabilities (hereafter, environmental-covariate models), with the same categorical covariates for recapture probabilities as in the most parsimonious categorical-covariates CJS model. Weather variables included average daily temperature (°C) and average daily precipitation (mm) of each trapping interval between two successive trapping weeks. Daily temperatures and precipitation were not significantly correlated (Pearson's $r = 0.21$, $P = 0.29$). A quadratic term of precipitation was included in the CJS model to test the nonlinear effects of precipitation on survival. We used the minimum number of animals alive (MNA) to index the population size of *O. dauurica* (Krebs, 1999). We also used analysis of deviance (ANODEV) to estimate percent variation in survival probability explained by precipitation and temperature as effect sizes (Skalski et al., 1993).

The Pradel JS models for *O. dauurica* had the same combinations of covariates for survival probability (hereafter, survival submodel) and recapture probability (hereafter, recapture submodel) as those of the best and competing environmental-covariate CJS models (Pradel, 1996; White & Burnham, 1999). We built different JS models by including different combinations of temperature, precipitation, and MNA for the recruitment rate (hereafter, recruitment submodel). We then used AICc and Akaike weight to select the best and competing models to infer the effects of temperature, precipitation, and density on recruitment. We also built additional survival submodels with weather variables only. If density was included in the recruitment submodel but not in the survival model of the most parsimonious or a competing model, we concluded that changes in population size exerted stronger effects on recruitment than on survival. We used the variable importance index to compare the strength of the effect of a covariate between survival and recruitment. The variable importance index of a covariate to survival or recruitment is computed as the sum of Akaike weights over the models, of which the survival or recruitment submodel includes the covariate (Burnham & Anderson, 2002). The greater the index value, the more important the covariate. To assess the net effects of weather and increases in population size on population growth rates, we built the Pradel-λ JS models with the identical survival and recapture probability submodels as the most parsimonious CJS model. The Pradel-λ JS model also includes population growth rates (λ;

hereafter, the λ submodel). We modeled λ as a function of different combinations of population size, temperature, linear and quadratic terms of precipitation, and MNA. The CJS and JS models were built with the program MARK version 7.1 (White & Burnham, 1999). All covariates, including weather variables, were included in the design matrix in MARK (White & Burnham, 1999).

We computed mean weekly population growth rates using the formula: $\text{pgr} = [\ln(\text{MNA}_t) - \ln(\text{MNA}_{t-1})]/\text{weeks}$, where pgr is the mean weekly population growth rate; ln() is the natural logarithm function; MNA_{t-1} and MNA_t are the minimum numbers of animals alive at time $t-1$ and t, respectively; and weeks is the number of weeks between $t-1$ and t. We also used generalized least square (GLS) models to test for quadratic relationships between population growth rates and precipitation with order-1 autocorrelative error (Pinheiro & Bates, 2000).

Results

We captured 293 pikas (2010: 110; 2011: 85; and 2012: 98) over 28 trapping weeks from 2010 to 2012. Minimum numbers of animals alive fluctuated seasonally (Fig. 1a). Annual mean sex ratios (male/female) ranged from 0.62 to 0.86 (Fig. 1b). Our trapping data met the CJS model assumptions [test 2CT: male, $N(0,1) = -1.54$, $P = 0.12$; female, $N(0,1) = -1.91$, $P = 0.06$; test 3SR: male, $N(0,1) = 0.24$, $P = 0.81$; female, $N(0,1) = 0.28$, $P = 0.78$]. The median c hat was 1.12 for the CJS model. The best categorical-covariate CJS model had time-dependent, sex-independent survival probabilities but time- and sex-independent recapture probabilities (Akaike weight $w = 0.65$). The second best model with time- and sex-independent survival and time-independent, sex-dependent recapture probabilities had $\Delta\text{QAICc} = 2.01$. Weekly survival fluctuated seasonally, ranging from 0.74 to 0.96 (Fig. 2). We used time- and sex-independent recapture probabilities in the environmental-covariate CJS models.

The best environmental-covariate CJS model included population size (i.e., MNA; coefficient $= -0.035$, 95% confidence interval (CI) $= -0.052$ to -0.018) and precipitation (coefficient $= -3.436$, 95% CI $= -4.931$ to -1.942; $w = 0.51$). The second best models included population size (coefficient $= -0.027$, 95% CI $= -0.053$ to 0.002), precipitation (coefficient $= -2.929$, 95% CI $= -4.943$ to -0.916), and temperature (coefficient $= -0.011$, 95% CI $= -0.038$ to 0.017; $w = 0.25$, $\Delta\text{QAICc} = 1.45$). The third best model had ΔQAICc of 2.43. Population size explained 26% of variability in survival probabilities ($P \leq 0.01$), linear effects of precipitation 11% ($P = 0.09$), and temperature 37% ($P \leq 0.01$). Therefore, we used two combinations of covariates for the survival submodel of the JS models: (1) population size and precipitation and (2) population size, precipitation, and temperature, plus another survival submodel with precipitation and temperature as the only covariates.
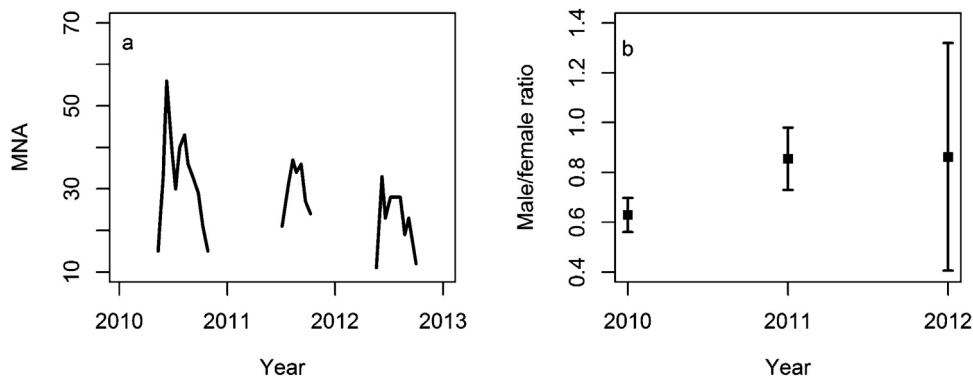
Fig. 1. (a) Minimum number of animals alive (MNA) and (b) annual mean sex ratios (male/female) of Daurian pikas in Naren, Abaga Qi, Inner Mongolia, China from May 2010 to October 2012.
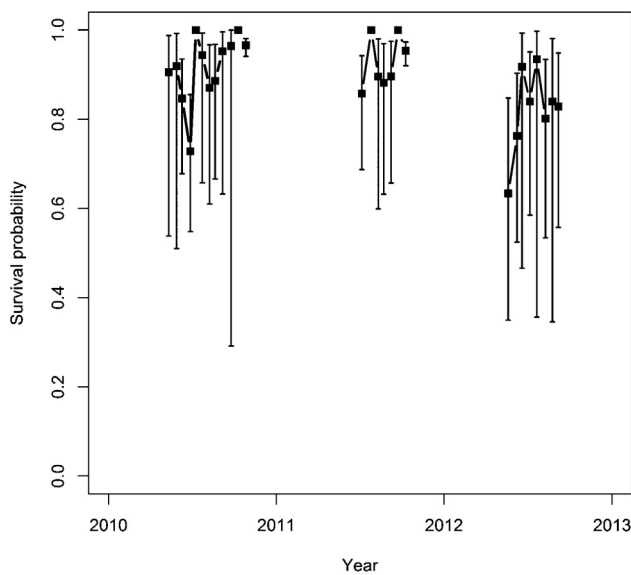

Fig. 2. Estimates of weekly survival probabilities of Daurian pikas in Naren, Abaga Qi, Inner Mongolia, China from May 2010 to October 2012. The estimates were generated by the full time-dependent survival model [$\phi(t)$]. Vertical bars are 95% CIs.

Fig. 3. Nonlinear relationship between population growth rates and precipitation in generalized least-squares models for Daurian pikas in Naren, Abaga Qi, Inner Mongolia, China from May 2010 to October 2012.

The CJS model including density and linear and quadratic precipitation terms had the ΔQAICc value of 0.82 as a competing model. The quadratic effects of precipitation explained 25% of variability in survival probabilities ($P \leq 0.01$).

Population size was included in the recruitment submodel of the best and two competing JS models (ΔAICc < 2.0, Table 1), with the 95% CI of the coefficient excluding zero and the variable importance index of 0.87 (Table 2). In contrast, population size was included only in the survival submodel of the third best model, with 95% CI of the coefficient including zero and the variable importance index of 0.18 (Tables 1 and 2). Precipitation was included in the recruitment submodel of the second best model with the 95% CI of the coefficient including zero and the variable importance index of 0.29 (Table 2). The effects of temperature had different signs on survival (negative) and recruitment
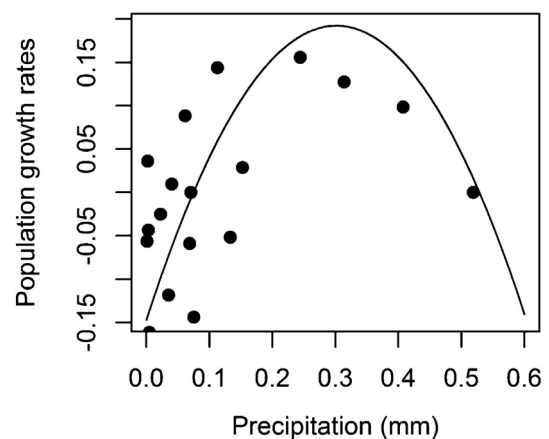
(positive), whereas population size and precipitation had negative effects on survival and recruitment (Table 2).

The most parsimonious Pradel-λ JS model had population growth rate (λ) as a function of population size (coefficient = -0.002, 95% CI = -0.004 to -0.006), temperature (coefficient = -0.002, 95% CI = -0.003 to -0.005), and linear (coefficient = 0.876, 95% CI = 0.252–1.500) and quadratic terms (coefficient = -0.200, 95% CI = -2.921 to -0.277) of precipitation (Akaike weight = 0.61). The second best Pradel-λ model had ΔQAICc of 3.24. Population growth rates were a quadratic function of precipitation in the GLS regression (linear term: $P = 0.01$; quadratic term: $P = 0.04$; Fig. 3).

Discussion

Ecological and demographic mechanisms underlying animal population dynamics involve the concomitant effects of weather and density on different vital rates (Coulson et al., 2005; Morrison & Hik, 2007). Population density and climate

Table 1. The Jolly–Seber models for the effects of temperature (temp; °C), precipitation (prec; mm), and population density (MNA) on weekly survival (ϕ) and recruitment (f) of Daurian pikas in Naren, Abaga Qi, Inner Mongolia, China from May 2010 to October 2012.

Model	AICc	ΔAICc	Akaike weights	Model likelihood	Number of parameters	Deviance
ϕ (temp + prec) p(.) f (temp + MNA)	3317.42	0.00	0.40	1.00	7	990.04
ϕ (temp + prec) p(.) f (temp + prec + MNA)	3318.07	0.65	0.29	0.72	8	988.63
ϕ (temp + prec + MNA) p(.) f (temp + MNA)	3319.08	1.66	0.18	0.44	8	989.64
ϕ (temp + prec + MNA) p(.) f (temp + prec + MNA)	3319.77	2.34	0.12	0.31	9	988.26
ϕ (prec + MNA) p(.) f (temp + MNA)	3325.73	8.30	0.01	0.02	7	998.34
ϕ (prec + MNA) p(.) f (temp + prec + MNA)	3327.13	9.71	0.00	0.01	8	997.69
$\phi(t)$ p(.) $f(t)$	3339.53	22.11	0.00	0.00	54	907.30

Note: AICc and ΔAICc are Akaike information criterion corrected for small sample size and difference in AICc between the model and the most parsimonious model.

affect the population dynamics and the vital rates of pikas (*Ochotona* spp.) (Kreuzer & Huntly, 2003; Morrison & Hik, 2007; Pech et al., 2007). Increased temperatures had complex effects on the demography of *O. dauurica*: negative effects on survival; positive effects on recruitment; and negative net effects on population growth rates. Precipitation affected population growth rates of *O. dauurica* through its nonlinear (quadratic) effects on survival probabilities, supporting the optimum precipitation hypothesis. Furthermore, increases in population size had stronger negative effects on recruitment than on survival of *O. dauurica*; therefore, density-dependent feedbacks to recruitment may serve as a main regulatory mechanism of the population dynamics of *O. dauurica* like in other small mammals (Reed & Slade, 2008).

Population abundance indices and survival probabilities of *O. dauurica* varied from the beginning to the end of plant growing seasons from 2010 to 2012 (Figs. 1 and 2). Furthermore, the breeding season of *O. dauurica* is relatively short, beginning in April, peaking between May and June, and terminating by the end of July or early August (Chen et al., 2014). Peak population sizes of the studied *O. dauurica* population slightly declined from 2010 to 2012 (Fig. 1a). From July 2009 to November 2009, we live-trapped *O. dauurica* on a site 6.5 km northeast of the 2010 trapping plot. However, *O. dauurica* on the 2009 trapping plot went locally extinct in a radius of about 5 km during the winter of 2009 (L. Chen, unpublished data). *O. dauurica* populations often undergo local extinctions during the winter (Formozov, 1966). Winter

climate affects adult survival of collared pikas (*O. collaris*) (i.e., offspring recruits; Morrison & Hik, 2007). Our findings of the effects of changes in weather and population size are restricted to the spring–autumn demographics and population dynamics. Populations of *O. princeps* exhibit metapopulation dynamics, with the spatiotemporal dynamics of local colonization and extinction on the habitat patches (Moilanen et al., 1998). However, we are not certain whether *O. dauurica* populations are metapopulations on our site. Long-term mark-recapture studies on multiple sites are needed to better understand spatial population dynamic patterns of *O. dauurica*.

Survival probabilities of talus-dwelling pikas (such as *O. princeps*) in North America are greater than those of burrow- or grassland-dwelling pikas, including *O. dauurica* (Smith, 1988). *O. princeps* can live up to 6 years, whereas burrow-dwelling pikas have an ecological lifetime of about 2 years or less (Smith, 1988; Wangdwei et al., 2013). Mean monthly survival probabilities of plateau pikas (*O. curzoniae*), another burrow-dwelling pika, are 0.69 for spring and 0.28 for summer (Wangdwei et al., 2013). Compared to talus-dwelling pikas in North America, *O. dauurica* is closer to the fast end of the slow–fast life history continuum, with greater litter sizes, shorter lifetimes, and more fluctuating population dynamics (this study; Dobson & Oli, 2007; Smith, 1988).

There is a growing body of evidence of nonlinear effects of climate on the demography and dynamics of birds and mammals (Ballerini et al., 2009; Lima et al., 2002; Nevoux

Table 2. Estimates of the Jolly–Seber model coefficients measuring the effects of temperature (°C), precipitation (mm), and density on weekly survival and recruitment of Daurian pikas in Naren, Abaga Qi, Inner Mongolia, China from May 2010 to October 2012.

Model	ΔAICc	Akaike weight	Temperature (survival)	Precipitation (survival)	Density (survival)	Temperature (recruitment)	Precipitation (recruitment)	Density (recruitment)
M1	0.00	0.40	**−0.04**	**−2.47**		**0.11**		**−0.13**
M2	0.65	0.29	**−0.04**	**−2.06**		**0.13**	−1.31	**−0.15**
M3	1.66	0.18	**−0.03**	**−2.75**	−0.01	**0.11**		**−0.14**

Note: AICc and ΔAICc are Akaike information criterion corrected for small sample size and difference in AICc between the model and the most parsimonious model.
Words in parentheses refer to submodels for survival and recruitment, respectively. Numbers in bold stand for 95% confidence interval below or above zero (i.e., excluding zero). Models M1, M2, and M3 are the top three models in Table 1.

et al., 2008). The quadratic effects of precipitation on population growth rates and survival suggest optimal moisture condition or precipitation for *O. dauurica* in the semi-arid grassland (Fig. 3). Initial increases in precipitation probably improve habitat conditions in a semi-arid area and thus enhance *O. dauurica* survival. Nevertheless, *O. dauurica* lives in underground burrows. Rainwater beyond optimal precipitation may drown adult *O. dauurica* and newborns inside burrows (X.R. Wan, personal observation). Excess rainfall seems to be detrimental to the demography of small mammals in arid or semi-arid regions. For example, increased rainfall reduces survival of African multimammate rats (*Mastomys natalensis*) in African arid land (Julliard et al., 1999). Increased winter precipitation lowers winter–spring population growth rates of Mongolian gerbils (*Meriones unguiculatus*) in western Inner Mongolia, China (Wang & Zhong, 2006). Likewise, summer rainstorms flood food caches of *Dipodomys spectabilis* and result in local extinctions of *D. spectabilis* in the Chihuahua Desert, Arizona, USA (Valone et al., 1995). Nonlinear responses of populations to precipitation, a limiting ecological factor in semi-arid areas, may raise concerns with the future fate of *O. dauurica* under future global change, which is predicted with potential increases in precipitation and temperatures in northern latitudes, particularly in high elevations (IPCC, 2007).

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