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

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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.

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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.

Keywords: Density dependence; *Ochotona dauurica*; Pika; Population dynamics; Recruitment; Small herbivorous mammals; Survival probability

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