Habitat Alteration Influences a Desert Steppe Lizard Community: Implications of Species–Specific Preferences and Performance

7 authors, including:

Shu-Ran Li
Chinese Academy of Sciences

5 PUBLICATIONS   **12** CITATIONS

SEE PROFILE

Travis R. Robbins
Northern New Mexico College

18 PUBLICATIONS   **97** CITATIONS

SEE PROFILE

Wei-Guo Du
Chinese Academy of Sciences

90 PUBLICATIONS   **1,187** CITATIONS

SEE PROFILE

Habitat Alteration Influences a Desert Steppe Lizard Community: Implications of Species-Specific Preferences and Performance

Author(s): Zhi-Gao Zeng , Jun-Huai Bi , Shu-Ran Li , Yang Wang , Travis R. Robbins , Shao-Yong Chen , and Wei-Guo Du

Habitat Alteration Influences a Desert Steppe Lizard Community: Implications of Species-Specific Preferences and Performance

Zhi-Gao Zeng[1], Jun-Huai Bi[2], Shu-Ran Li[1], Yang Wang[1], Travis R. Robbins[3,4], Shao-Yong Chen[2], and Wei-Guo Du[1,5]

[1] Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China
[2] College of Life Sciences, Inner Mongolia Normal University, Hohhot, Inner Mongolia 010022, China
[3] Department of Biology, Pennsylvania State University, University Park, PA 16802, USA

Abstract: Understanding community assembly is a fundamental goal of ecology and evolutionary biology, because it provides insight into how a given landscape changes in a synergistic fashion. With the current background of global environmental change, studies of how habitat alteration affects local communities often focus on species' responses to community-level changes instead of responses to specific ecological factors that elucidate the roles each factor plays in the final synergistic response. Here, we focus on the specific ecological mechanisms that drive changes in community structure. We investigated compositional patterns of lizard communities among natural and altered habitats (vegetatively sparse, natural, and dense) in the desert steppe ecosystem of Inner Mongolia, China. Habitat alteration induced significant changes in community composition of lizards and was associated with significant changes in both biotic and abiotic niches. Our preference (soil, thermal, and prey) and performance (locomotor, antipredator, and competitive) experiments identified many of the biotic and abiotic factors shaping lizard community responses to habitat change. In the natural habitat, where *Phrynocephalus frontalis* and *Eremias multiocellata* codominate, *P. frontalis* experienced low overlap (across lizard species) in preferred prey. *Eremias multiocellata* preferred the thermal environment of the natural habitat (and dense habitat), but this one factor did not fully explain its codominance. *Phrynocephalus frontalis* dominated in the sparse habitat, where this lizard species experienced its preferred tight soil and warm thermal environment and experienced low overlap of preferred prey. In the dense habitat, where *E. argus* dominates, *P. frontalis* and *E. multiocellata* exhibited impeded locomotor performance, whereas *E. argus* was not impeded by vegetation density. *Eremias argus* also preferred the thermal environment of the dense habitat (and natural habitat). Our results suggest, furthermore, that adult predation risk was not a major determinant of community divergence among habitats and that competition likely plays a more important role. Interspecific competition for microhabitat use may explain the low abundance of *E. argus* in the natural habitat and the low abundance of *P. frontalis* in the dense habitat. Overall, our assessment of lizard preferences and performances explained community composition across habitats. Our focus on ecological mechanisms associated with habitat alteration highlights the importance of vegetation conservation in lizard community management.

Key words: Community divergence; Competition; Conservation; Diet; Habitat structure; Locomotion; Predation; Reptile; Soil porosity; Temperature

THE ECOLOGICAL mechanisms generating community structure have attracted much scientific attention since the 1970s (e.g., Pianka 1973; Morris et al. 1989; Wellborn et al. 1996) and remain a key issue in modern community ecology (Gotelli 2000; Sanderson 2004; Hausdorf and Hennig 2007). In the last few decades, investigators have developed many theories—such as niche theory, interspecific competition theory, and neutral theory—to explain the coexistence of species within a community (Tilman 2004; Sutherland 2011). Patterns of species composition and abundance have also been compared along environmental gradients, and manipulative experiments have been conducted to identify causes of community divergence (Wellborn et al. 1996; Pike et al. 2011; Pelegrin and Bucher 2012). These studies provide invaluable insight into the general rules of community formation and maintenance, yet large gaps in our understanding remain with regard to how specific interactions of biotic and abiotic factors drive species assemblages and change communities.

Because of the pervasive effect of ongoing global change on biodiversity (Tilman et al. 2001; Dirzo and Raven 2003), explaining how environmental changes affect community structure and composition is a pertinent focus of modern community ecology. Studies increasingly demonstrate that anthropogenic activities such as urbanization, agriculture, and overgrazing have greatly altered plant composition, and in turn imposed significant impacts on local animal communities (e.g., altering species composition and abundance; Taylor and Fox 2001; Pawar et al. 2004; Attum et al. 2006; D'Cruze and Kumar 2011; Pelegrin and Bucher 2012). Clarifying the ecological mechanisms that underlie community change and divergence is essential for our understanding of how habitat alteration influences local communities. Despite the critical importance of exploring ecological mechanisms, the majority of habitat alteration studies focus only on conservation implications for managing disturbed habitats, with little effort on mechanism identification (Taylor and Fox 2001; D'Cruze and Kumar 2011).

Lizards are excellent model organisms for analyzing community structure and assemblage, because they exhibit several characteristics that make them conducive to study, including ample morphological diversity, ease of observation and capture, and relatively high abundance (Huey et al. 1983; Pianka 1986). More importantly, lizards have been extensively studied such that we know many of the biotic and abiotic factors that influence their behavior and physiology, leading to preferences and performance characteristics associated with different habitats. As such, preferences of environmental factors, such as soil characteristics, thermal environments, and available prey often influence where species are found (Zaady and Bouskila 2002; Lelièvre et al. 2011). Habitat-specific fitness of behavioral, physiological, and life history traits also can determine species within a

[4] Present Address: Department of Biology, Chemistry, and Environmental Science, Northern New Mexico College, Espanola, NM 87532, USA
[5] Correspondence: e-mail, duweiguo@ioz.ac.cn

community (McLaughlin and Roughgarden 1989; Petren and Case 1998; Irschick and Losos 1999). These include traits such as locomotor performance and outcomes of interspecific interactions, including predation and competition (Wellborn et al. 1996; Higham and Russell 2010; Lisičić et al. 2012). In this study, we specifically examine the influence of environmental, physiological, and behavioral factors on community divergence after habitat alteration. We test three factors associated with lizard preference (soil, thermal, and prey) and three associated with lizard performance (locomotor, antipredator, and competitive). We test the following hypotheses in the desert steppe ecosystem of Inner Mongolia, China, where three sympatric species of lizard occur. The Mongolian racerunner (*Eremias argus*) is an oviparous lacertid lizard generally occupying grassy sand dunes and thicket. The multiocellated racerunner (*Eremias multiocellata*) is a viviparous lacertid species living generally in arid or semiarid regions covered by sparse vegetation. The steppe toad-headed agama (*Phrynocephalus frontalis*) generally inhabits desert, semidesert, or grassland with low and sparse vegetations (Zhao et al. 1999).

Preference Hypotheses

Physical properties of soil, which are largely dependent on vegetation (Huang et al. 2007), may affect burrow selection of lizard species (Zaady and Bouskila 2002). *Phrynocephalus frontalis* is adept at digging and has obvious burrow orifices, whereas *E. argus* and *E. multiocellata* are capable of digging, although often the entrances of the burrows are obscured. As a result of each species burrowing where it can best meet its dwelling requirements, community divergence could occur if different lizard species prefer to burrow into different types of soil.

Environmental temperature is important for the maintenance of key physiological and behavioral processes in reptiles (Huey 1982) and has been shown to influence microhabitat use of reptiles (Du et al. 2006; Lelièvre et al. 2011). If lizard species differ in preferred thermal ranges, they may select habitats with a suitable thermal environment to optimize these processes, leading to compositional divergence among habitats.

Dietary differences are important in structuring some lizard fauna (James 1991; Manicom and Schwarzkopf 2011), and food-based habitat partitioning has been described among sympatric lizards (Saenz 1996; Daly et al. 2008). If preferred prey of lizard species is habitat-specific, community divergence could emerge as a consequence of each species foraging, where it experiences the least niche overlap and can best meet its dietary requirements.

Performance Hypotheses

Locomotor performance may determine a species' success in avoiding predators and foraging (Pough 1989; Garland and Losos 1994; Miles 2004) and thus may influence which habitats a species occupies. In the field, the sprint speed of lizards is not only determined by their own morphology and physiology but also depends on the substrates in different microhabitats (Higham and Russell 2010; Collins et al. 2013). The occupation of nonpreferred microhabitats can be associated with reduced locomotor performance in lizards. As such, lizards with high values of sprint sensitivity may avoid habitats in which performance is submaximal (Irschick and Losos 1999; López and Martín 2013). Consequently, lizards with different abilities of locomotion and maneuverability may occupy different habitats, which maximize locomotor performance and therefore individual fitness.

Birds are important predators for many lizards, and thus can influence lizards' habitat selection (or occupancy; McLaughlin and Roughgarden 1989; Roches et al. 2011). Because birds are predominately visually oriented (López and Martín 2013), predation risk is likely different in habitats providing different amounts of shelter and different for each lizard species based on body size, appearance, and microhabitat use. Therefore, predation could be an important driver shaping compositional divergence in lizard communities.

Interspecific competition has been shown to drive segregation among broad vegetation types and in the use of habitat components in many assemblages of lizards (e.g., Case and Bolger 1991; Petren and Case 1998; Lisičić et al. 2012). Compositional divergence in lizard communities could arise if each species is competitively dominant in different habitats, restricting other species' access to those areas.

Natural habitat in the desert steppe ecosystem recently has been altered for the purpose of agriculture (cash crops) and conservation (desertification control), creating three distinct structural habitats along a gradient from low, sparse vegetation to tall, dense vegetation. In this study, we first investigated compositional patterns of the lizard community among the contrasting structural habitats. We then designed field experiments to identify ecological causes of any compositional divergence. Habitat alteration in our study region serves as a "natural experiment," providing a unique opportunity to explore the ecological mechanisms of lizard community divergence in arid ecosystems.

Materials and Methods
Study System

We carried out the study at Ordos Key Research Station for Field Observation of Ecological Environments on Sandy Grassland, managed by the Ministry of Agriculture, the People's Republic of China (Fig. 1). The Station (40°12′17″N, 111°07′43″E; elevation 1,036 m) is located in Jungar Banner of Inner Mongolia, a cold, semiarid region. The mean annual temperature is 6–7°C with a maximum of 39.1°C in July and a minimum of −32.8°C in January. The average annual precipitation is 300–380 mm with most of the rain falling between July and September (Zeng et al. 2014).

The study area is predominantly sandy grassland of moderately low and sparse vegetation, mainly including *Artemisia ordosica*, *A. sphaerocephala*, *Agriophyllum pungens*, *Inula salsoloides*, and *Poa sphondylodes*. Much of this natural habitat, dominated by *A. ordosica*, has been altered since the early 2000s, for agricultural purposes (cash crops, such as herba ephedra [*Ephedra sinica*], and alfalfa [*Medicago sativa*]) and to combat desertification (e.g., by planting introduced drought-enduring species including sweetvetch [*Hedysarum leave*, *H. scoparium*], korshinsk peashrub [*Caragana korshinskii*], and erect milkvetch [*Astragalus adsurgens*]). These vegetation changes have created habitats varying in vegetative structure from more
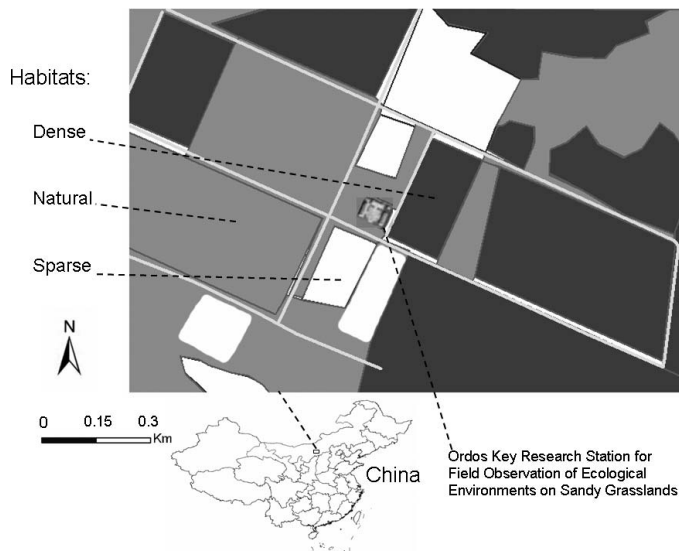
Fig. 1.—Map of our study area in the desert steppe of Inner Mongolia, China, showing the distribution of three distinctive habitat structural types based on vegetative density: sparse, natural, and dense. Map redrawn from CNES spot image taken by CNES/Astrium in 2014, available at http://www. google.cn/maps/.

sparse to more dense. Compared to the original (natural) habitat, human-altered habitat that is now dominated by *E. sinica* has become vegetatively sparser and lower (henceforth sparse habitat) and that dominated by *H. leave* is denser and higher (henceforth dense habitat; Figs. 1, 2).

We confirmed the differences in habitat structure by surveying the vegetation present in each habitat in 2012 (Fig. 2). Three 1 × 1–m plots were positioned at 25 points (around each lizard pitfall trap array, see below) spaced 30 m apart in a grid pattern in each habitat. The vegetation height and the proportions of basal cover, bare ground, and litter were estimated and recorded in each plot by the point frame method (Cook and Box 1961). We determined differences among habitats in these variables with the use of one-way ANOVAs. We analyzed all data with the software package SPSS (v19.0, SPSS Inc., Chicago, IL), and reported all values in the text as ranges followed by mean ± SE in parentheses.

Across the three habitats, the lizard community consists of three species: *E. argus*, *E. multiocellata*, and *P. frontalis*. Our 2012 surveys showed that body size of adult lizards, measured as snout–vent length (SVL) and body mass (BM), was largest for *E. multiocellata* (SVL, 4.29–7.44 cm [6.25 ± 0.05]; BM, 3.49–10.03 g [6.37 ± 0.12]; n = 128) and smallest for *P. frontalis* (SVL, 4.02–5.75 cm [4.71 ± 0.03]; BM, 2.77–8.21 g [4.14 ± 0.07]; n = 159), with *E. argus* (SVL, 4.99–8.72 cm [5.73 ± 0.02]; BM, 2.85–6.82 g [4.31 ± 0.04]; n = 288) in between. Potential avian predators of these lizards include the grey shrike (*Lanius excubitor*), magpie (*Pica pica*), red-footed falcon (*Falco amurensis*), kestrel (*Falco tinnunculus*), and cuckoo (*Cuculus canorus*; Zhao et al. 1999; Qiao et al. 2011).

Composition of the Lizard Community

We surveyed lizard species presence and abundance in each of the three habitats (sparse, natural, and dense) both in 2011 and 2012. During July, August, and September of 2011, we randomly set up three 30 × 30–m quadrats (spaced 100 m
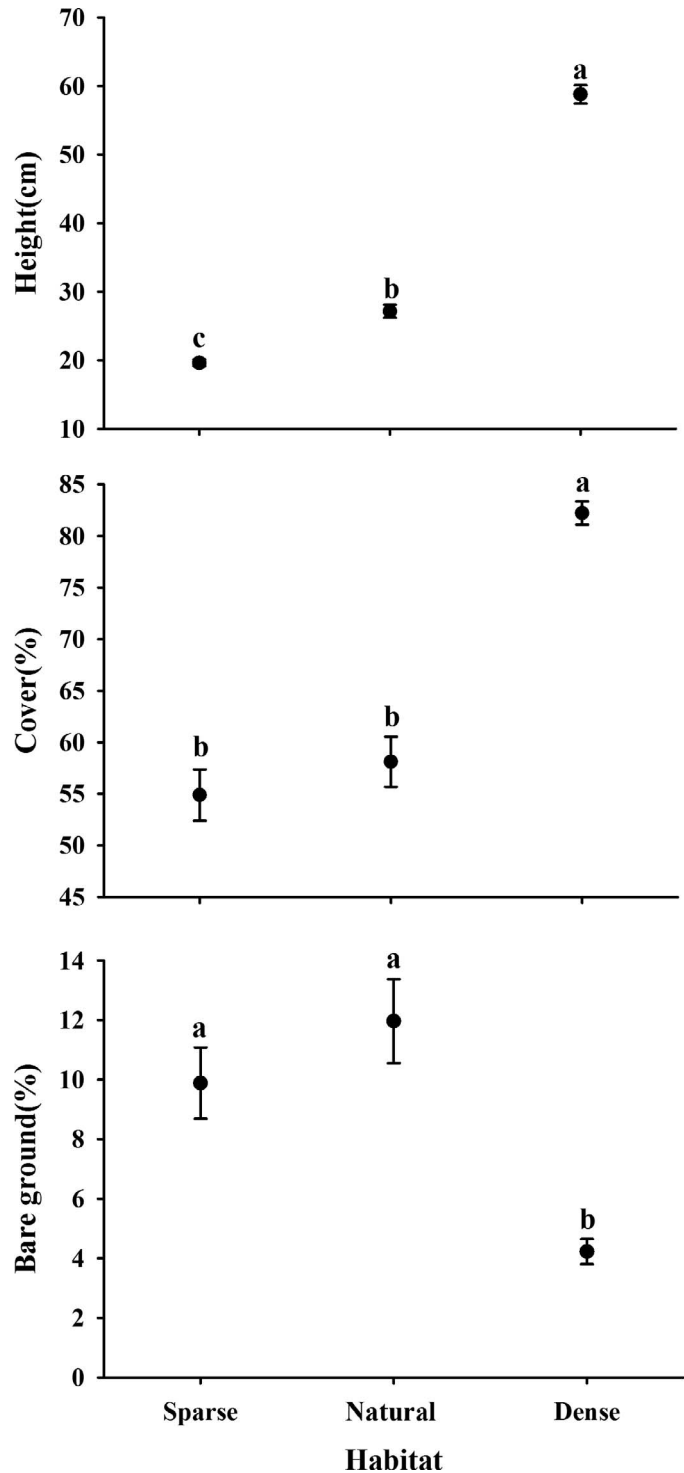
Fig. 2.—Vegetation height, percent basal cover, and percent bare ground in three focal habitats (sparse, natural, and dense) at the study site. Points represent means and error bars represent ±1 SE. Means with different letters above the error bars are statistically different (Tukey's tests).

apart) for sampling lizards at two sites (separated by at least 500 m) in each habitat. We searched for lizards and captured them by hand or noose in each quadrat for 1 h between 0900 and 1300 h, 1 d per month. During June, July, and September of 2012, we surveyed lizard species presence and abundance with the use of pitfall traps in each of the

three contrasting habitats (sparse, natural, and dense; separated by at least 500 m). In each habitat, we placed 25 pitfall trap arrays (spaced 30 m apart). Each array consisted of four buckets (25 cm diameter × 35 cm deep) arranged in a Y shape (one at the center and three at the ends), with 4-m-long × 0.3-m-high steel sheet drift fences running between the central bucket and the three ends (see Nogueira et al. 2005). We conducted field surveys for seven consecutive days and nights per month, for a total of 21 survey days per habitat. We inspected the lizard trap arrays from 0700 to 1900 h, during which the lizards were active. The captured lizards were marked by toe clipping, measured for SVL with a ruler to 1 mm, weighed for BM with an electronic scale to 0.01 g, and then released at the capture site. Recaptures were excluded from our analyses of lizard community composition. We used a crosstabs Chi-square test to compare differences in relative abundances of lizard species among habitats.

Preference Experiments

Soil preference.—We first determined differences in soil characteristics among habitats, and then used these results to inform our preference experiment. Ten sites in each habitat were randomly selected to sample soil for the analysis of soil porosity. In the field during the active season (May–September), we found that the burrowing depth of *P. frontalis* was 13.3–30.0 cm (19.8 ± 1.1, *n* = 20) for burrows with an obvious orifice. Therefore, at each site we took one intact soil core both at the surface layer (0–5 cm) and the subsurface layer (15–20 cm) with the use of a foil sampler. We analyzed the soil samples with standard methods, as described in the Soil Analysis Book (Nanjing Institute of Soil Science 1980). We determined dry weight of the soil by oven-drying the cores at 105°C for 24 h. We used the following equation to calculate soil total porosity:

$$P_t = \left(1 - \frac{B_d}{d_s}\right) \times 100$$

where P_t is the total soil porosity (%); B_d the soil bulk density (g cm^{-3}), defined as the dry weight of soil per unit volume of soil; and d_s the soil density (g cm^{-3}), assumed to be 2.65 g cm^{-3}. We determined differences among habitats in soil porosity with the use of *t*-tests and one-way ANOVAs.

We conducted soil preference trials in the field. In total, we used 21 *E. argus*, 21 *E. multiocellata*, and 20 *P. frontalis* in the soil preference experiment. These adult lizards were recently and randomly collected from our study site and measured for SVL and BM prior to the experiment. We constructed 10 plastic terraria (60 × 30 × 40 cm [L × W × H]), the bottoms of which were covered with 15-cm-deep soil. Half (30 × 30 cm, L × W) of each terrarium was covered with soil from the sparse habitat and half from the dense habitat. The soil in each terrarium was generally composed of four large clumps, two from the sparse habitat and two from the dense habitat. Soil characteristics of each large clump were not changed when the soil was removed from the habitat. The gap between the large clumps was covered by small clumps of soil. Characteristics of the soil covered the gap had some change, but this small change had not obvious impact on the results. We did not include soil from the natural habitat because it was similar in soil porosity to

soil from the dense habitat (see Results). We introduced the lizards (*n* = 62 total) individually into the plastic terraria between 1000 and 1400 h on sunny days. We checked them once every hour. We interrupted the trial once the experimental lizard burrowed into soil to hide. The soil choice (burrowing into soil) by the animal was recorded. We assessed soil preference for burrowing with a crosstabs chi-square test comparing proportions of each lizard species burrowing in each soil type.

Thermal preference.—In the field, we measured operative temperatures randomly across habitats and the amount of time each species utilized sun and shade for thermoregulation. In July and September of 2012, we randomly scattered 10 hollow copper models of lizards (each containing a thermochron i-Button temperature logger; DS1921, MAXIM Integrated Products Ltd., USA) to measure operative temperatures (Bakken 1992) every hour in each habitat during the 7-d trapping period. We used repeated-measures ANOVAs to determine among-habitat differences in operative temperatures with temperature records from the copper models at different hours as the repeated measures.

To identify the microhabitats at which each species was active in the field, we searched for lizards during daylight from 0800 to 1800 h in the three habitats. Once detected, we allowed a lizard 2 min to habituate to our presence and then observed each lizard for 20 min. We recorded the amount of time that each lizard spent in the open sun and in shade (Daly et al. 2008). We estimated activity time of each lizard in each microhabitat by the proportion of time observed in the sun and under shade. We used two-way ANOVAs to determine among-habitat and among-species differences in the activity time of lizards in the shade and the sun.

We conducted trials in the laboratory to determine preferred body temperatures for each species. In total, we collected 57 adult lizards (20 *E. argus*, 19 *E. multiocellata*, and 18 *P. frontalis*) from our study site in September 2012 and housed them individually in plastic terraria (60 × 30 × 40 cm, L × W × H). Food (mealworms, *Tenebrio molitor*) and water were provided *ad libitum*. We suspended two 100-W light bulbs above one end of each terrarium to create a temperature gradient from 20°C to 55°C for thermoregulation by lizards. We measured cloacal temperatures as body temperatures (T_b) of active lizards (*n* = 57 total) every 2 h from 0800 to 1800 h with the use of a UNI-T UT325 digital thermometer (Uni-Trend Technology, China Limited, Guangdong, China). For each lizard, we collected 11 or 12 T_b measurements within 2 d. For each species, we used the average values of all the upper and lower limits of the selected temperatures to represent its setpoint temperature (T_{set}) range. We also calculated the mean of the central 50% temperature recordings as the preferred body temperature of lizards (Hertz et al. 1993). We used one-way ANOVAs to determine among-species differences in preferred body temperature.

Prey preference.—For each lizard species, we assessed availability of invertebrate prey, measured prey consumption, and estimated prey preference and dietary overlap associated with each habitat. We used small pitfall traps and sweep netting to sample invertebrates, the main dietary component of these lizards, in the three habitats. We positioned invertebrate pitfall traps (*n* = 25/habitat) at 25

points (around each lizard trap array) in each of the three habitats. Pitfall traps were 25-mm diameter plastic buckets buried up to their top edge in soil that were half filled with a solution of water and detergent. In June, July, and September of 2012, we left the pitfall traps open during the day for 1 wk per month, collecting prey each day. We closed the traps at night to reduce any potential confounding by nocturnal invertebrates to which the diurnal lizards would not have access. We also collected invertebrate samples by sweep netting the foliage (0–1 m above the ground) at 25 2 × 2–m plots (around each lizard pitfall trap array) in each habitat (Stamps and Tanaka 1981). We collected 75 samples of 210 sweeps (10 sweeps per day) in the three habitats for the total of 21 survey days in 2012. Invertebrate samples by the pitfall traps and sweep netting were transferred to 70% ethanol and returned to the laboratory for sorting.

Stomach contents were identified to determine the prey eaten by the three species of lizards. We collected stomach samples from adult lizards in all three habitats in June, July, and September of 2012. Lizards were captured by hand from 1100 to 1600 h on sunny days so that they would likely have had the opportunity to feed before capture. Lizards were weighed for BM, and then euthanized shortly after capture by injection of sodium pentobarbitone (60 mg ml^{-1}) into the abdominal cavity and preserved immediately in 70% ethanol. In the laboratory, we removed the stomachs from preserved lizards and collected a total of 86, 66, and 135 stomach samples (n = 287 total) with prey for *E. argus*, *E. multiocellata*, and *P. frontalis*, respectively. We measured lizard SVL and stomach mass before analysis of stomach contents. To assess lizard diets, we separated stomach contents in a Petri dish, identified prey remains with the use of a dissecting microscope, and then scored the frequencies of different prey types in each individual sample. We used a crosstabs chi-square test to compare differences in diet composition among the lizard species. We used ANCOVA to compare the difference in stomach mass among species as well as among individuals from the three habitats with BM of lizards as the covariate.

We used the following Manly's alpha Selection Index (α; Chesson 1983) to evaluate the importance of each prey category for the three lizard species in different habitats (i.e., prey preference):

$$\alpha_i = \frac{r_i}{n_i} \frac{1}{\sum_{j=1}^{m}(r_j/n_j)}$$

where α_i = Manly's Selection Index for prey types i; r_i, r_j = proportions of prey types i and j in the diet (i and j = 1, 2, 3,...,m); n_i, n_j = proportions of prey types i and j available; m = number of potential prey types. What Manly refers to as prey species is analogous to prey types in this study. A prey was used selectively if the selection index did not equal 1. If selected, a prey was preferred when $\alpha_i > 1$, and avoided when $\alpha_i < 1$.

Because prey availability is influenced by prey consumption, predicting relative abundances of the lizard species based on prey preference and availability may be unreliable. Thus, we assessed overlap in diet of consumed and preferred prey between lizard species in each habitat. We assumed that lower overlap would reflect potential for greater fitness.

We evaluated diet similarity between pairs of lizard species by using Pianka's index of dietary overlap:

$$O_{jk} = \frac{\sum_{i}^{n} P_{ij}P_{ik}}{\sqrt{\sum_{i}^{n} P_{ij}^{2} \sum_{i}^{n} P_{ik}^{2}}}$$

where P_{ij} and P_{ik} are the proportions of the ith prey item used by each lizard species j and k, respectively (Pianka 1973). Values of overlap vary between 0 (no overlap) and 1 (complete overlap). Values of paired species were summed to assess overall overlap (complete overlap thus = 2) specific to each species and the differences between species greater than or equal to 0.6 ($\Delta O \geq 0.6$) were considered to be potentially biologically meaningful (Pianka 1976).

Performance Experiments

Locomotor performance.—To evaluate the effect of habitat on locomotor performance of lizards, we set up 30 cm-wide raceways by using two steel sheeting fences (300 × 30 cm, L × H) carved through the vegetation of the three habitats. In total, we used 18 field-caught adults for each species of *E. argus*, *E. multiocellata*, and *P. frontalis* in the locomotor performance tests. These lizards (n = 54 total) were measured for SVL and BM at the beginning of the test, then placed in individual wooden containers (55 × 32 × 38 cm, L × W × H) and left undisturbed for at least 30 min to acclimate to ambient temperature prior to each trial. The locomotor performance of lizards is dependent on body temperature, but it is formidable, if not impossible, to control the body temperature of lizards in a field experiment precisely. To minimize the temperature effect, we initialized all trials at 1400 h and finished before 1600 h on sunny days from 20 to 26 July 2012, during which the fluctuation in ambient temperature was relatively small. In addition, we measured body temperature of each lizard just before the locomotor performance test with the use of the UT325 digital thermometer so we could account for any influence in our statistical models. We assessed locomotor performance by chasing the lizards along the raceway with a paintbrush. If the tested lizard hid in the grass or ran in an inverse direction, we would test it again in the end. We tested each lizard at least twice in a habitat with a rest period of at least 30 min between the two trials. For each individual, we had two acceptable trials in a habitat. We calculated the running speed by dividing the length of racetrack (3 m) by the cumulative time taken by lizards to cross the end of the raceway. The fastest speed for each individual was then used to evaluate the locomotor capability of each species in each habitat. We tested for effects of SVL, BM, and body temperature on sprint speed using partial correlation or regression analyses. Partial correlation analyses indicated that the sprint speed of the lizards was not related to SVL (r = −0.044, P = 0.582, n = 159) after the effect of BM had been statistically removed. Regression analysis indicated that the sprint speed of lizards was related to BM ($F_{1,160}$ = 10.78, $P < 0.01$) but not to their body temperatures ($F_{1,160}$ = 0.04, P = 0.84). Accordingly, SVL and body temperature were not included in our statistical model to test for the among-habitat

difference in the sprint speed of lizards. We calculated the residual value of sprint speed relative to BM to remove the effect of body size on locomotor performance, and then used repeated-measures ANOVAs to assess the among-habitat difference in the sprint speed of three lizard species with species as the factor and sprint speed in each habitat as the repeated measures.

Performance under predation.—We evaluated predation risk for each lizard species by recording predation events in each habitat. In August of 2012, we set up three small enclosures ($2 \times 2 \times 0.3$ m, L $\times$ W $\times$ H) along a transect at intervals of 20 m in each habitat. We built enclosures by burying steel sheeting into the sand (10-cm depth). An infrared digital trail camera (Ltl 5210A, Shenzhen Smd Technology Co., Ltd., Guangdong, China) was fastened on a pole just outside each enclosure to record predation events. One adult lizard was introduced in each enclosure and exposed to natural predation for 3 d. We then retrieved the cameras and checked for photographs of lizards captured by predators. We used a crosstabs chi-square test to compare differences in predation risk of lizards ($n = 9$ individuals/ lizard species/habitat) among the three habitats.

Performance under competition.—Given the practical difficulty of evaluating competition in open field conditions, lizards in 12 square enclosures ($5 \times 5 \times 0.5$ m, L $\times$ W $\times$ H) in the natural habitat were observed to investigate their use of habitat on their own and when housed together with other species, as suggested by Daly et al. (2008). We modified the ground cover within the enclosures such that each one contained a clump of *A. ordosica* (100 cm in diameter), whereas the rest of the ground space was bare sand. We captured the experimental animals from sites at least 200 m away from the enclosures to reduce familiarity effects.

We placed the collected lizards in the enclosures within 24 h of capture and observed them in the following six combinations with equal sex ratios: (1) four *E. argus* in an enclosure ($n = 2$), (2) four *E. multiocellata* in an enclosure ($n = 2$), (3) four *P. frontalis* in an enclosure ($n = 2$), (4) two *E. argus* and two *E. multiocellata* in an enclosure ($n = 2$), (5) two *E. argus* and two *P. frontalis* in an enclosure ($n = 2$), and (6) two *E. multiocellata* and two *P. frontalis* in an enclosure ($n = 2$). Observations were carried out by two observers standing at a distance outside each enclosure after the lizards had been allowed to settle for 24 h. Observations were conducted twice per hour from 0800 to 1700 h for 15 continuous days in July of 2012, with each observation block lasting 20 min. July was the middle period of their active season; this time selection for the competition trials possibly decreased the seasonal effects. We recorded the amount of time that each lizard species spent in the clump of *A. ordosica* and bare sandy ground in each enclosure. We used repeated-measures ANOVAs to determine the effect of interspecific competition on habitat use of the three lizard species with habitat use of individuals on successive days as the repeated measures. In the analysis of each species, we included habitat type (bare ground vs. the clump) and three experimental treatments (single focal species and combination treatments with each of other two species) as the factors, and the percentage of time that the focal lizard spent in each habitat as the response variable.

Assessing Predictions across Experiments

We attempted to summarize the contribution of each factor to the community divergence observed across habitats but realize the possibility of covariation among the many components involved makes the true individual contribution of each factor unclear. Thus, we simply ranked lizard species in each habitat based on statistical differences. With regard to the particular performance or preference trait, a higher rank of a lizard species in a given habitat represents a better match to the habitat. With regard to lizard community composition, a higher rank means a higher abundance in the observed composition relative to the other lizard species. Soil preference ranks were based on preference trials, where a 1 denotes preference and −1 avoidance. Thermal preference ranks were based on matching environmental differences to thermal preference differences among species. For example, if one habitat was significantly warmer and one species had a significantly higher preferred body temperature, then it was a match. Prey preference ranks were based on the sum of values of overlap with each other species in preferred diets in each habitat (see Table 2). Antipredator and locomotor performance ranks were based on significant differences among lizard species within each habitat. We summed the ranks across experiments for each species within each habitat, such that a higher rank would reflect more preferences and better performances in the associated habitat. Thus, the final summed rankings reflect the expected relative abundances in each habitat based on habitat-specific preferences and performances of each species.

Competitive interactions play an important role in shaping community structure in plant and animal communities (Schoener 1983; Goldberg and Barton 1992; Gurevitch et al. 1992; Petren and Case 1998; Lisičić et al. 2012), but changes in behavior due to competitive interactions within versus between species are difficult to assess with regard to cost and benefit. Intraspecific competition could be stronger or weaker than interspecific competition, such that differences in behavior between intra- and interspecific interactions may have positive or negative effects on the focal species. Confirming whether interspecific competitive effects are costly or beneficial is difficult without measuring an associated fitness-based effect. We can infer interspecific competitive effects, however, based on community assemblage in a post hoc fashion. As such, we assess the results of our competition experiment with regard to discrepancies between the observed community composition and the expected composition based on the sum of ranks across the experimental results. Furthermore, we summed habitat-specific results for each species across the biotic and abiotic factors identified by the preference and performance experiments.

RESULTS

Habitat Alteration

Land-use change for economic and conservational purposes profoundly changed the characteristics of vegetation in terms of height, basal cover, and bare ground. The sparse and natural habitats were shorter ($F_{2,222} = 439.07$, $P < 0.01$) and had less basal cover ($F_{2,222} = 50.16$, $P < 0.01$) than the dense habitat (Fig. 2). The sparse and natural
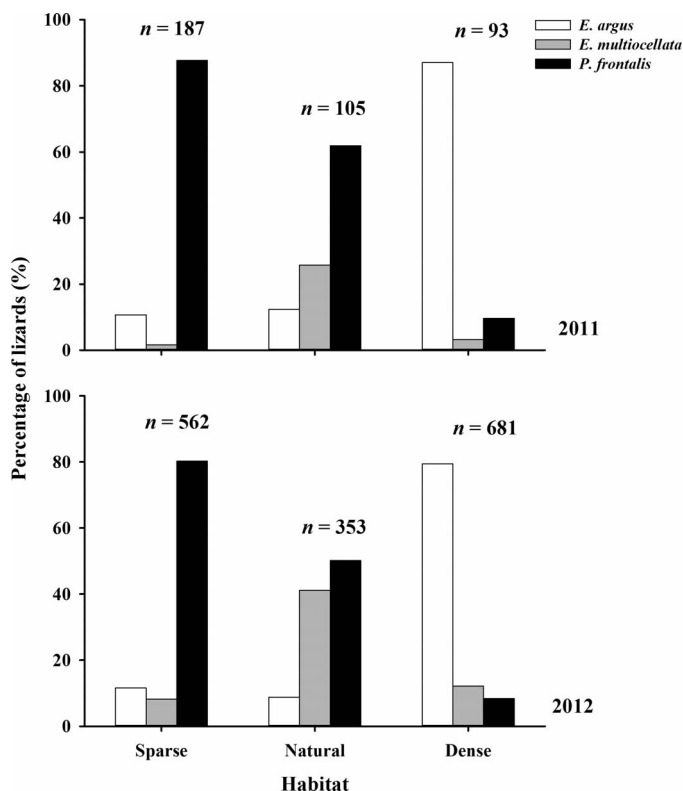
FIG. 3.—Composition of the lizard community based on specimens captured (*n*) in sparse, natural, and dense habitats in the desert steppe of Inner Mongolia, China in 2011 and 2012.

habitats also had a greater proportion of bare ground than the dense habitat ($F_{2,222} = 13.39$, $P < 0.01$; Fig. 2).

Composition of the Lizard Community

Habitat alteration induced significant changes in community composition of lizards. The community composition differed among the three habitats in both 2011 ($\chi^2 = 247.77$, $df = 4$, $P < 0.0001$) and 2012 ($\chi^2 = 995.41$, $df = 4$, $P < 0.0001$; Fig. 3). In the natural habitat, *P. frontalis* and *E. multiocellata* were the two dominant species, whereas *E. argus* was rare. By contrast, *E. argus* became dominant in the habitat with dense vegetation, whereas *P. frontalis* dominated in the habitat with sparse vegetation. Notably, lizard communities had similar compositions in a given habitat between the 2 yr (Fig. 3). We review the results of individual preference and performance experiments below but leave the assessment of their cumulative effects on community composition for the discussion.

Preference Experiments

Soil preference.—Soil porosity differed among the three habitats at both surface (sparse habitat, 28.2–38.4%, 33.6 ± 0.5, n =30; natural habitat, 31.3–45.9%, 36.3 ± 0.5, n = 30; dense habitat, 30.9–42.0%, 37.0 ± 0.4, n = 30; $F_{2,87} = 14.52$, $P < 0.0001$) and 15-cm depth (sparse habitat, 27.5–40.8%, 33.1 ± 0.6, n = 30; natural habitat, 31.2–43.4%, 36.9 ± 0.5, n = 30; dense habitat, 32.8–44.1%, 37.3 ± 0.5, n = 30; $F_{2,87} = 19.28$, $P < 0.0001$), with less porosity in the sparse habitat than the other two habitats. The natural and dense habitats had similar soil porosity (surface, $t = -1.181$, $df = 58$, $P = 0.243$; 15-cm depth, $t = -0.696$, $df = 58$, $P = 0.489$).
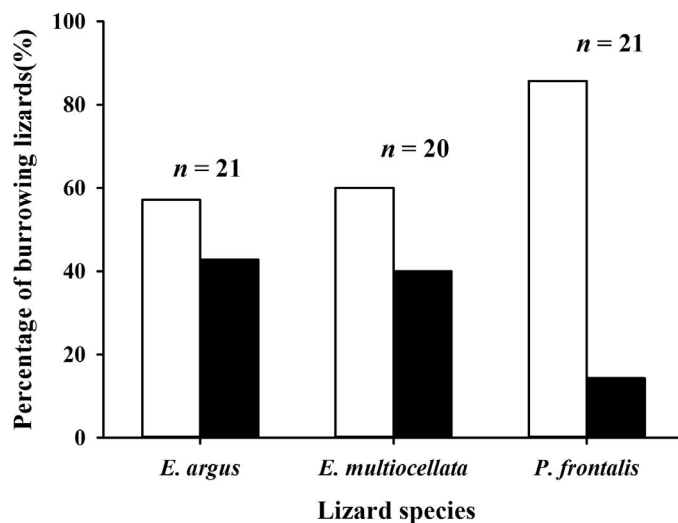

FIG. 4.—Preference for burrowing in soil from the sparse (open bars) and dense (black bars) habitats by *Eremias argus*, *E. multiocellata*, and *Phrynocephalus frontalis* in the desert steppe of Inner Mongolia, China. The preference exhibited by *P. frontalis* to burrow in soil of the sparse habitat is statistically significant.

The physical properties of soil influenced lizards' selection of soil for burrowing, as shown by divergent soil preference in the three species ($\chi^2 = 8.47$, $df = 2$, $P = 0.015$). *Phrynocephalus frontalis* preferred to burrow in soil from the sparse habitat ($\chi^2 = 12.80$, $df = 1$, $P = 0.0003$), but *E. argus* and *E. multiocellata* showed no preference of soil type (*E. argus*, $\chi^2 = 0.05$, $df = 1$, $P = 0.827$; *E. multiocellata*, $\chi^2 = 1.19$, $df = 1$, $P = 0.275$; Fig. 4).

Thermal preference.—In July, mean operative temperatures did not differ among the habitats ($F_{2,147} = 1.06$, $P = 0.35$), but the dense habitat was cooler in the morning and warmer in the afternoon than the sparse habitat ($F_{20,1470} = 2.64$, $P = 0.0001$; Fig. 5). In September, however, mean operative temperatures were higher in the sparse habitat than the natural and dense habitats ($F_{2,76} = 5.03$, $P = 0.009$; Fig. 5). Field observations showed that *E. argus* and *E. multiocellata* spent more time in shade ($F_{2,770} = 10.98$, $P < 0.0001$) and less time in full sun ($F_{2,770} = 25.41$, $P < 0.0001$) than did *P. frontalis*. The three lizard species spent more time in sun ($F_{2,770} = 4.85$, $P < 0.01$) and less time in shade ($F_{2,770} = 4.45$, $P = 0.01$) in the sparse habitat compared to the natural and dense habitats (Fig. 6).

In the laboratory, preferred body temperatures determined in a thermal gradient were lower in the two *Eremias* species (34.7–37.6°C, 35.8 ± 0.2, $n = 20$ for *E. argus*; 33.8–36.9°C, 35.7 ± 0.2, $n = 19$ for *E. multiocellata*) than in *P. frontalis* (35.4–38.7°C, 37.1 ± 0.2, $n = 18$; $F_{2,54} = 14.30$, $P < 0.0001$). The T_{set} range was similar between *E. argus* (34.6–36.9°C) and *E. multiocellata* (34.7–36.6°C), which was relatively low compared to that in *P. frontalis* (35.6–38.6°C).

Prey preference.—The three lizard species preyed primarily on insects from Formicidae, Hymenoptera, and Cicadellidae, with a preference for insect larvae (Fig. 7). Diet composition differed among the three species ($\chi^2 = 313.94$, $df = 16$, $P < 0.0001$). A difference occurred between *E. argus* and *E. multiocellata* ($\chi^2 = 16.12$, $df = 8$, $P = 0.04$), but especially between the genera *Eremias* and *Phrynocephalus* (Fig. 7). Larvae (>30% of the total used prey) were
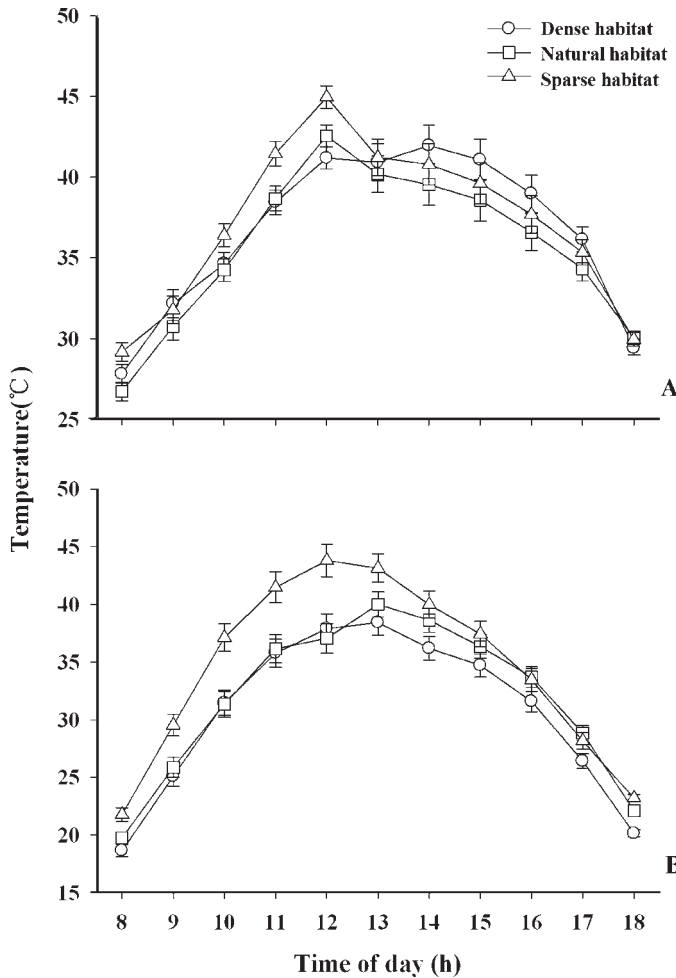
Fig. 5.—Mean operative temperatures in July (A) and September (B) at three different habitats for lizards in the desert steppe of Inner Mongolia, China.

the main prey of *E. argus* and *E. multiocellata* but were less commonly observed as prey of *P. frontalis*. Instead, *P. frontalis* consumed more formicids than the two *Eremias* species (Fig. 7).

The stomach mass varied among species ($F_{2,254} = 7.99$, $P < 0.001$), with heavier stomachs in *E. argus* (0.239–0.285 g, 0.262 ± 0.012, $n = 79$) and *P. frontalis* (0.235–0.271 g, 0.253 ± 0.009, $n = 125$) than in *E. multiocellata* (0.162–0.218 g, 0.190 ± 0.014, $n = 60$), but differences were nonsignificant among habitats in all three species of lizards ($F_{2,254} = 0.42$, $P = 0.66$), after the effect of their BM was removed. Prey preference of the dominant lizard species in each habitat did not match prey availability and abundance of that habitat. Formicids, preferred by *P. frontalis*, were not abundant in the sparse habitats where the lizard species were dominant. Although *P. frontalis* did not prefer hymenopterans, *P. frontalis* was dominant in the sparse habitat where hymenopteran abundance was highest (19.47% compared to 5.10% in the dense habitat). Similarly, *E. argus* did not prefer larvae, but *E. argus* was dominant in the dense habitat where larvae were more abundant (than in the natural habitat; 19.26% vs. 3.17%). In addition, carabids were preferred by *E. argus* and *E. multiocellata*, but also not abundant in the field. Insects from Tenebrionidae were
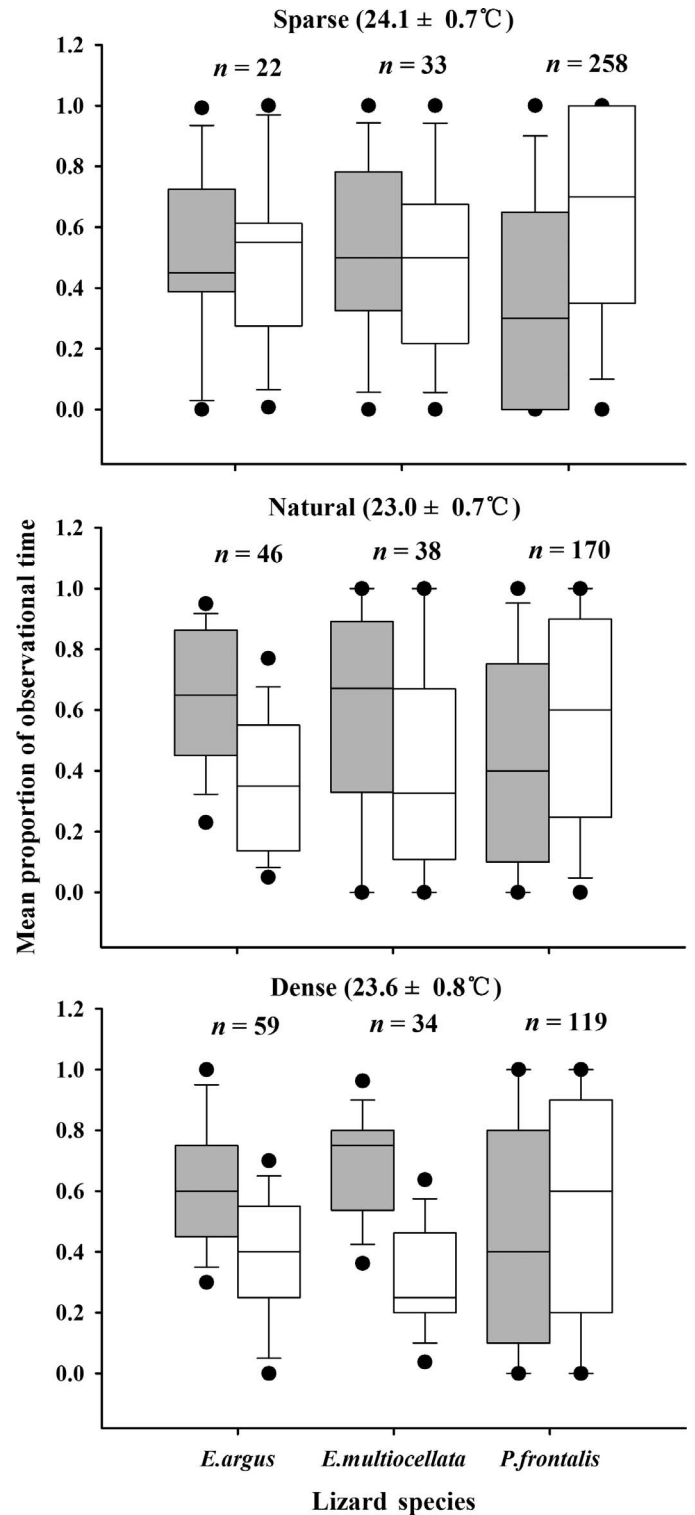
Fig. 6.—The proportion of time (mean ± 1 SE) spent in the sun (white bars) and shade (black bars) by *Eremias argus*, *E. multiocellata*, and *Phrynocephalus frontalis* in the desert steppe of Inner Mongolia, China. The proportions of time observed in the sun and under shade are averaged from measurements recorded during lizard observations. Mean daily temperatures of each habitat from May to September are in parentheses after each habitat title.
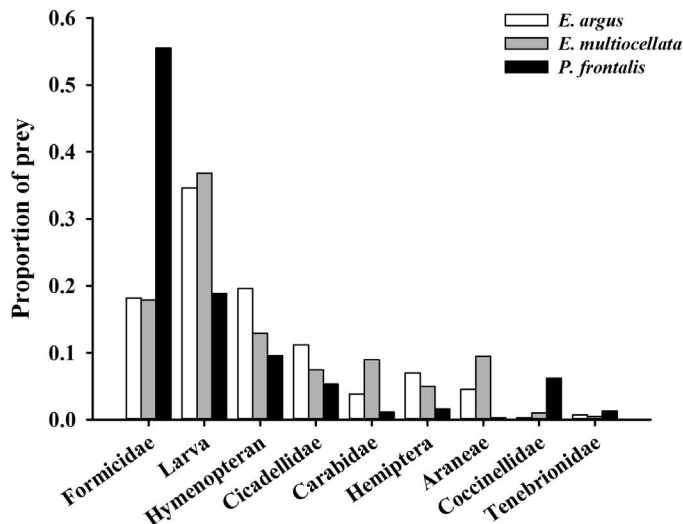
FIG. 7.—Overall diet composition of *Eremias argus, E. multiocellata*, and *Phrynocephalus frontalis* in the desert steppe of Inner Mongolia, China. The category Larva consists of multiple insect species.

abundant in the sparse and natural habitats, and coccinellids were abundant in the natural habitat, but these prey were not preferred by the three lizard species (Table 1).

Diet overlap was lowest among all three lizard species in the natural habitat, where we also observed the greatest differentiation in paired diet overlap measures (Table 2). Overlap in diet was consistently high between the *Eremias* species in all three habitats for both all prey (>87%) and preferred prey (>90%; Table 2). *Phrynocephalus frontalis* thus had the lowest overlap in diet among the three species in each habitat, having what is considered biologically meaningful ($\Delta O \geq 0.6$) competitive release in the natural habitat.

Performance Experiments

Locomotor performance.—The sprint speed of lizards differed among habitats ($F_{2,102} = 42.82$, $P < 0.0001$), and the three lizards performed differently in each habitat, as indicated by the significant interaction between habitat and species ($F_{2,102} = 3.73$, $P < 0.01$). Further analysis on each species found that the sprint speed declined with the increasing vegetation coverage of habitats for *P. frontalis* ($F_{2,34} = 16.06$, $P < 0.0001$) and *E. multiocellata* ($F_{2,34} = 37.51$, $P < 0.0001$) but not for *E. argus* ($F_{2,34} = 2.82$, $P = 0.074$; Fig. 8). As a result, *E. argus* ran faster in the dense habitat than did *P. frontalis* and *E. multiocellata* ($F_{2,51} = 4.06$, $P = 0.02$) but not in the natural ($F_{2,51} = 0.35$, $P = 0.70$) or sparse ($F_{2,51} = 1.67$, $P = 0.20$) habitats (Fig. 8).

Performance under predation.—Direct evidence from field experiments showed that the predation risk of lizards decreased as vegetation coverage increased ($\chi^2 = 12.084$, $df = 2$, $P = 0.002$; Fig. 9). Predation risk did not differ, however, among the three lizard species in each habitat (sparse vegetation, $\chi^2 = 0.900$, $df = 2$, $P = 0.638$; natural vegetation, $\chi^2 = 0.386$, $df = 2$, $P = 0.825$; dense vegetation, $\chi^2 = 2.077$, $df = 2$, $P = 0.354$).

Performance under competition.—We detected an effect of competitor presence on microhabitat use for two of the lizard species. In field enclosures, *P. frontalis* spent more time on bare ground than under the clump of *A. ordosica* ($F_{1,128} = 91.32$, $P < 0.0001$), whereas the two *Eremias* species used the clump more than bare ground (*E. argus*, $F_{1,58} = 196.5$, $P < 0.0001$; *E. multiocellata*, $F_{1,68} = 277.6$, $P < 0.0001$). Microhabitat use was affected by the presence of another species in *P. frontalis* ($F_{2,128} = 3.89$, $P = 0.02$) and *E. argus* ($F_{2,58} = 5.39$, $P < 0.01$). *Phrynocephalus frontalis* spent more time on bare ground when *E. argus* was present while *E. argus* spent more time in the clump when *E. multiocellata* was present. By contrast, *E. multiocellata* microhabitat use was not affected by presence of other species ($F_{2,68} = 2.28$, $P = 0.11$; Table 3).

DISCUSSION

Habitat alteration drove divergence of the lizard community in the desert steppe, with one species (*E. argus*) dominating in dense habitat but another (*P. frontalis*) in sparse habitat (Fig. 3). Our experimental data support the conclusion that the lizard community composition of each habitat was influenced by multiple preference and performance traits associated with individual lizard species.

TABLE 1.—Composition (%) of available prey and diet selection (expressed as Manly's alpha Selection Index α) of the three lizards *Eremias argus*, *E. multiocellata*, and *Phrynocephalus frontalis* in the sparse, natural, and dense habitats in the desert steppe of Inner Mongolia, China. If selected, a prey was preferred when $\alpha_i > 1$ (bold) and avoided when $\alpha_i < 1$. The category Larva consists of multiple insect species.

|	Prey items								
Vegetation	Formicidae	Hymenopteran	Coccinellidae	Larva	Cicadellidae	Carabidae	Tenebrionidae	Hemiptera	Araneae
Composition of available prey									
Sparse	0.340	0.195	0.059	0.320	0.046	0.003	0.017	0.017	0.003
Natural	0.675	0.044	0.139	0.032	0.079	0	0.020	0.008	0.004
Dense	0.669	0.051	0.011	0.193	0.043	0.003	0.006	0.023	0.003
Selective index of *E. argus*									
Sparse	0.812	0.449	0	**4.084**	**1.694**	**2.173**	0	0.306	0.134
Natural	**1.023**	0.180	0	**1.981**	**1.313**	**2.073**	0	0.341	0.089
Dense	0.486	**4.480**	0	0.713	0.471	0.101	0.223	0.324	0.203
Selective index of *E. multiocellata*									
Sparse	0.909	0.287	0	**4.571**	0.812	**2.431**	0	0	0.600
Natural	**1.632**	0.281	0	**1.732**	0.308	**2.724**	0.054	0.142	0.126
Dense	0.450	**3.497**	0	0.830	0.585	0.745	0	0.342	0.551
Selective index of *P. frontalis*									
Sparse	**4.227**	0.191	0.175	**3.336**	0.171	0.027	0.028	0.026	0.007
Natural	**5.036**	0.191	0.607	0.104	0.950	0	0.084	0.022	0.007
Dense	**2.963**	**1.859**	0.025	**1.050**	0.441	0.053	0.236	0.343	0.031
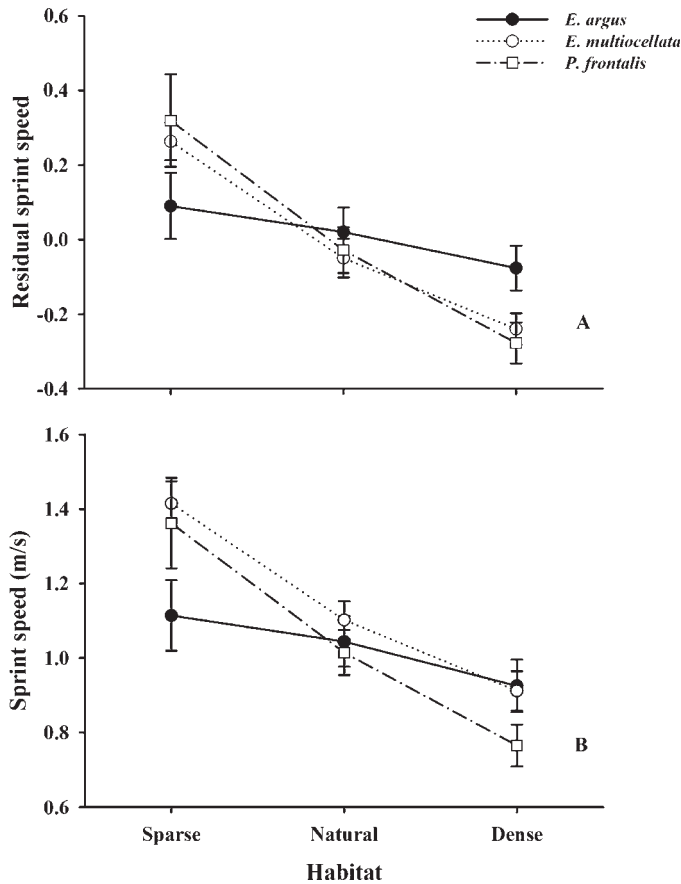
FIG. 8.—Locomotor performance of *Eremias argus*, *E. multiocellata*, and *Phrynocephalus frontalis* in the sparse, natural, and dense habitats in the desert steppe of Inner Mongolia, China. Residuals of sprint speed were derived relative to individual lizard body mass. Sample sizes were 18 for each species.

Phrynocephalus frontalis preferred the compact soil and warm thermal environments found in the sparse habitat where this lizard species was dominant. Also, the prey types preferred by *P. frontalis* in the sparse habitat had less overall overlap than the preferred prey of the two *Eremias* species. *Eremias argus* exhibited maximal locomotor performance and preference for the thermal environment in the dense habitat, where it was dominant. *Eremias multiocellata* had its highest abundance in the natural habitat, where it was codominant with *P. frontalis*. The natural habitat provided a thermal environment appropriate for *E. multiocellata* and little overlap of prey for *P. frontalis* compared to both *Eremias* species (Tables 2, 4). Competition (for microhabitat use) in the presence of *E. multiocellata* may drive the low abundance of *E. argus* in the natural habitat.

The different survey methods between 2011 and 2012 were confounded with potential year effects on the lizard estimates. However, the similarity of lizard composition pattern between the 2 yr indicated that the estimates were robust to the survey method and year effects. Our results are consistent with other studies in finding that changes in vegetation can influence the structure of lizard communities. For example, both small and large scales of exogenous disturbances on vegetation may cause considerable change in community composition and species abundance of lizards
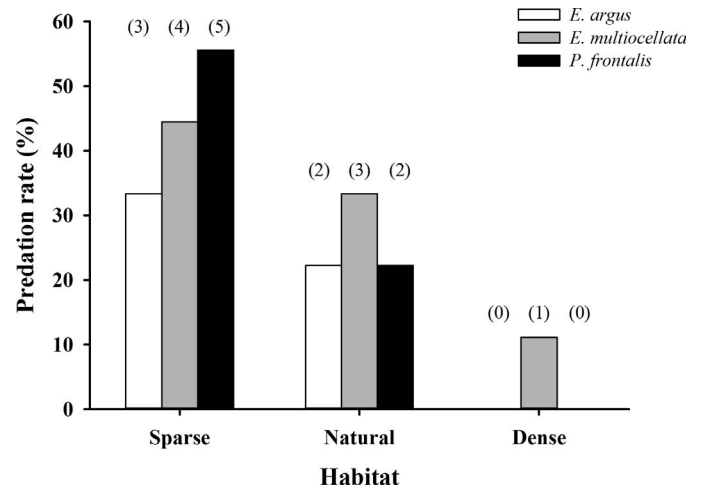

FIG. 9.—Predation risk of *Eremias argus*, *E. multiocellata*, and *Phrynocephalus frontalis* in three habitats in the desert steppe of Inner Mongolia, China. We collected nine lizard samples for each species from each habitat to analyze predation rate. The numbers in parentheses show the actual numbers of lizards depredated.

(Taylor and Fox 2001; Attum et al. 2006; Scott et al. 2006; Pike et al. 2011). Indeed, habitat alteration can have profound effects on the community composition of a variety of animals, from insects to mammals, that directly or indirectly rely on local vegetation. These impacts are not only evident across natural environmental gradients resulting from community succession (Towns and Elliott 1996; Pelegrin and Bucher 2012; Steen et al. 2013), but also across habitats recently changed due to human activities and climate warming (Pawar et al. 2004; D'Cruze and Kumar 2011; Gallucci et al. 2012; Li et al. 2014).

Despite the well-known effects of habitat alteration on lizard communities, the mechanisms underlying these habitat-induced changes are rarely resolved. Our experiments explored how both biotic and abiotic factors associated with lizard preference (e.g., soil properties, thermal environment, and prey) and performance (e.g., locomotor performance, predator avoidance, and interspecific competition) shape the divergence of lizard communities. In general, lizard preferences for soil in which to burrow, body temperatures, and prey items appear to affect community composition across habitats, as well as habitat-

TABLE 2.—Overlap (expressed as Pianka's index) in both all prey and preferred prey by frequency of occurrence among *Eremias argus*, *E. multiocellata*, and *Phrynocephalus frontalis* in each of the three habitats from the desert steppe of Inner Mongolia, China.

	All prey			Preferred prey		
	Habitat			Habitat		
	Sparse	Natural	Dense	Sparse	Natural	Dense
Species pairs						
E. argus, *E. multiocellata*	0.877	0.972	0.965	0.940	0.976	0.973
E. argus, *P. frontalis*	0.624	0.276	0.706	0.641	0.286	0.709
E. multiocellata, *P. frontalis*	0.662	0.422	0.671	0.720	0.430	0.689
Sums						
E. argus	1.500	1.248	1.671	1.580	1.261	1.682
E. multiocellata	1.538	1.393	1.636	1.660	1.406	1.662
P. frontalis	1.285	0.698	1.377	1.360	0.715	1.398

TABLE 3.—Changes in habitat use due to competitive interactions for *Eremias argus*, *E. multiocellata*, and *Phrynocephalus frontalis* in the desert steppe of Inner Mongolia, China. The percentage of time that a lizard spent under vegetation or bare sandy ground was measured [range (mean ± 1 SE)]. The experimental treatments with bold font signify statistically significant differences.

| | | | Habitat use (% time) | |
No. of focal lizards	Focal lizard species	Competitive treatments	Bare sandy ground	Clump of *Artemisia ordosica*
15	*E. argus*	*argus*	0.00–58.82 (28.60 ± 4.16)	41.18–100.00 (71.40 ± 4.16)
10	***E. argus***	***argus* + *multiocellata***	**0.00–50.00 (16.87 ± 5.10)**	**50.00–100.00 (83.13 ± 5.10)**
7	*E. argus*	*argus* + *frontalis*	0.00–90.00 (26.67 ± 6.10)	10.00–100.00 (73.33 ± 6.10)
16	*E. multiocellata*	*multiocellata*	0.00–78.95 (20.37 ± 5.28)	21.05–100.00 (79.63 ± 5.28)
14	*E. multiocellata*	*multiocellata* + *argus*	0.00–83.33 (19.19 ± 5.65)	16.67–100.00 (80.81 ± 5.65)
7	*E. multiocellata*	*multiocellata* + *frontalis*	0.00–75.00 (10.79 ± 7.99)	25.00–100.00 (89.21 ± 7.99)
26	*P. frontalis*	*frontalis*	0.00–100.00 (69.15 ± 7.13)	0.00–100.00 (30.85 ± 7.13)
24	***P. frontalis***	***frontalis* + *argus***	**0.00–100.00 (78.65 ± 7.42)**	**0.00–100.00 (21.35 ± 7.42)**
17	*P. frontalis*	*frontalis* + *multiocellata*	0.00–100.00 (64.07 ± 8.82)	0.00–100.00 (35.93 ± 8.82)

specific locomotor performance and interspecific competition for microhabitat use. Predation rates were similar among species in each habitat, suggesting that the risk of predation for adults did not affect community composition across habitat types. Below we discuss in turn the impact of each factor on lizard community divergence to elucidate the underlying ecological mechanisms further.

TABLE 4.—Summary of habitat-specific results for each species across the preference and performance traits examined. Ranks are relative based on statistical differences. Ranks associated with competition are not included in the sum of ranks, because they were assigned based on observed compositions (post hoc). Further bases of rankings and assessment are explained in the methods. Additionally, we present two subsummaries of the habitat-specific results, respectively based on the abiotic (soil, thermal, and locomotor substrate) and biotic (prey, predation risk, and competition) factors.

| Rank summary matrix | | | | |
| | | | Habitat | |
Traits	Species	Sparse	Natural	Dense
Preference traits				
Soil	*Eremias argus*	0	0	0
	E. multiocellata	0	0	0
	Phrynocephalus frontalis	1	−1	−1
Thermal	*E. argus*	0	1	1
	E. multiocellata	0	1	1
	P. frontalis	1	0	0
Prey	*E. argus*	0	0	0
	E. multiocellata	0	0	0
	P. frontalis	0	1	0
Performance traits				
Locomotor	*E. argus*	0	0	1
	E. multiocellata	0	0	0
	P. frontalis	0	0	0
Predation risk	*E. argus*	0	0	0
	E. multiocellata	0	0	0
	P. frontalis	0	0	0
Sum of ranks	*E. argus*	0	1	2
	E. multiocellata	0	1	1
	P. frontalis	2	0	−1
Observed composition	***E. argus***	**1**	**1**	**2**
	E. multiocellata	**1**	**2**	**1**
	P. frontalis	**2**	**2**	**1**
Competition (space) post hoc performance assessment	*E. argus*	0	−1	0
	E. multiocellata	0	0	0
	P. frontalis	0	0	−1
Subsum of ranks (for abiotic factors)	*E. argus*	0	1	2
	E. multiocellata	0	1	1
	P. frontalis	2	−1	−1
Subsum of ranks (for biotic factors)	*E. argus*	0	−1	0
	E. multiocellata	0	0	0
	P. frontalis	0	1	−1

Preference Hypotheses

We found partial support for the hypothesis that soil properties determine habitat selection of lizards and therefore shape community divergence. In our study system, the effect of altered vegetation on soil properties was evident, with loose soil in dense and natural habitats but tight soil in sparse habitats. Although the two *Eremias* lizards had no preference for soil properties, the toad-headed agama, *P. frontalis*, preferred to dig and burrow in the tight, sandy soil associated with the sparse habitat, where it is the dominant species, but avoided the loose soil from the dense and natural habitats.

Why does *P. frontalis* prefer the tight soil found in sparse habitat? The mechanical composition of soil can be an important ecological axis along which different lizard communities distribute in the desert (Shenbrot et al. 1991). *Phrynocephalus frontalis* constructs abundant burrows on open sandy surfaces as shelters from predators and as a refuge from extremely high temperatures (Zhao et al. 1999). Soil surface stability (tight soil crusts) may provide better support for the entrance of these burrows (Zaady and Bouskila 2002). The looser soil of the dense and natural habitats likely restricts burrow construction in *P. frontalis*, although it does not preclude its occupancy.

The hypothesis that each study species exhibits preferences for different thermal environments and selects the habitats that maximize access to them was also supported. The thermal environment influences the ecology of lizards because it affects many whole-body functions like feeding, mobility, and reproduction (Huey 1982), all of which can shape community composition of lizards in a diversity of habitats from desert to forest (Adolph 1990; Du et al. 2006; Daly et al. 2008; Lelièvre et al. 2011). In our desert system, the sparse habitat was warmer (at least in autumn and hence likely in spring) than the dense habitat (Fig. 5). Correspondingly, the dominant species in the sparse habitat, *P. frontalis*, had the highest preferred body temperature. It spent most of its time in the open sun, where it had access to higher temperatures throughout the day. By contrast, the dominant species in the dense habitat, *E. argus*, had a lower preferred body temperature, spent more time in shade, and shuttled frequently between patches of open sun and the cover of grass to maintain its preferred body temperature (Fig. 6). These findings suggest that the study species differ in their temperature preferences and thermoregulatory strategies

and select contrasting sparse or dense habitats that provide access to their preferred thermal environments.

The hypothesis that different distributions of preferred prey among the contrasting habitats result in lizard community divergence was weakly supported. We found that the three study species are insectivorous and that their diet composition and prey preference had a high degree of overlap (Tables 1, 2; Fig. 7). This is consistent with most natural lizard communities (Vitt et al. 2000; Manicom and Schwarzkopf 2011). Although other ecotherms like fish and snakes usually partition the food niche axis (Luiselli 2006; Colloca et al. 2010), most niche divergence in lizard communities occurs through partitioning the spatial and temporal niche axes (Luiselli 2008). However, the role of prey preference in habitat partitioning and community divergence was found in two species of agamid (congeneric) lizards in central Australia. In that system, *Ctenophorus isolepis* specializes in eating ants <5 mm long and selects *Spinifex*-dominated areas, whereas *C. nuchalis* prefers a diversity of prey available mostly in open areas (Daly et al. 2008). We found that *P. frontalis* experienced lower dietary overlap than the two *Eremias* species did with each other across habitats, experiencing potential competitive release in the natural habitat (Table 2). Preference for soil and thermal environments likely are stronger influences on the dominance of *P. frontalis* in the sparse habitat, but prey availability may be a factor in its codominance with *E. multiocellata* in the natural habitat.

Performance Hypotheses

Locomotor performance is closely related to the capability of escaping predation and gaining food, both of which determine individual fitness (Garland and Losos 1994; Miles 2004; Husak 2006). In our study, locomotor performance was habitat-specific and only differentiated among lizard species in the dense habitat where the most abundant species, *E. argus*, was also the fastest (Fig. 8). *Eremias argus* is rare in the other habitats, and thus our data support the hypothesis that lizards avoid habitats in which their performance is suboptimal (Irshick and Losos 1999).

Our results suggest more thickly vegetated habitat structure can physically impede locomotion (Crist and Wiens 1994; Tucker and McBrayer 2012; López and Martín 2013). We observed this effect in *P. frontalis* and *E. multiocellata*, which both showed decreased sprint speed across the range of sparse to dense vegetation. In contrast, the locomotor performance of *E. argus* was not impeded by the dense vegetation in which this species dominates (Fig. 8). The high abundance of *E. argus* in the dense habitat suggests it outcompetes the other two species, possibly by avoiding predation (although we did not detect any advantage) and/or acquiring food more efficiently. This advantage may be due to its excellent locomotion capability in this specific habitat.

Predators can differ among habitats in morphology and foraging behavior (McLaughlin and Roughgarden 1989; González-Suárez et al. 2011) and can determine the natural prey community accordingly. Predator–prey interactions are also influenced by habitat because habitat structure affects predation risk (López and Martín 2013). In our study, lizards were more conspicuous in sparse habitats than in dense habitats and had correspondingly higher predation risk from birds (Fig. 9). Predation risk between the three lizard species did not differ within any habitat, however, despite these lizards' differences in size, coloration, and movement pattern, all of which can affect the exposure of animals to avian predators (Zhao et al. 1999). Our results suggest that predation of adults is unlikely to be an important driver of community divergence in our study system. A possible explanation for this absence of among-species differences in predation is that these species have developed species-specific antipredation strategies to avoid avian predators effectively. We discuss how competition for microhabitat use influenced lizard community divergence below with respect to the synergistic influence of all the abiotic and biotic factors we examined in the desert steppe system.

Assessing Predictions across Experiments

Predictions of lizard community composition based on results across experiments were generally good (Table 4). In the sparse habitat, preferences for soil, thermal environment, and potential prey suggest that *P. frontalis* should be the most abundant species and the two *Eremias* species should be relatively rare, which is indeed the case (Tables 2, 4; Figs. 4, 6). In the natural habitat, all three preferences again play a role (Table 4), however, there is a discrepancy between predicted and observed community composition. *Phrynocephalus frontalis* is codominant with *E. multiocellata*, but our experiments suggest that *E. argus* should be codominant with *E. multiocellata* in the natural habitat (Table 4). *Eremias argus* is predicted to be more abundant than *P. frontalis* because of the thermal preference of *E. argus* and soil avoidance of *P. frontalis* (Table 4). The competition experiment may elucidate why *E. argus* is lower in abundance than expected in the natural habitat. The change in microhabitat use by *E. argus* in the presence of *E. multiocellata* may be costly for *E. argus* (Table 3); thus the relatively high abundance of *E. multiocellata* in the natural habitat may inhibit greater numbers of *E. argus*. Additionally, *P. frontalis* may exhibit higher abundance than expected because of competitive release experienced by the low overlap in preferred prey (Table 2). This biotic factor may be of greater biological significance than was assigned in our assessment. In the dense habitat, all three preferences again play a role, but here locomotor performance appears to also be influential (Table 4; Fig. 8). *Eremias argus* is predicted to be relatively abundant because of high locomotor performance and is indeed the most abundant species in the dense habitat. Additionally, competition may drive the low abundance of *P. frontalis* in the dense habitat because *P. frontalis* changes microhabitat use (with potentially negative effects) in the presence of *E. argus*, which is the most abundant species in the dense habitat. Thus, we found some evidence that competition (for microhabitat use) between lizard species contributes to compositional divergence of the lizard community after habitat alteration (Table 4).

A review of the literature suggests that the relative influence of abiotic and biotic factors may differ between ectothermic and homeothermic organisms; however, our results do not support a strong dichotomy (Table 4). Abiotic factors with regard to fish, such as pH, oxygen, salinity, and current velocity, and with regard to reptiles, such as substrate, rainfall, canopy cover and soil hardness, have been highlighted as important influences on ectotherm

community assemblage (Rahel and Hubert 1991; Taylor and Fox 2001; Selleslagh and Amara 2008; Pike et al. 2011; Schaffler et al. 2013), with temperature being a primary abiotic determinant (Jackson et al. 2001; Daly et al. 2008; Lelièvre et al. 2011; Schaffler et al. 2013). Biotic factors such as predation and competition, however, are often considered less important (McLaughlin and Roughgarden 1989; Arnott and Vanni 1993; Hacking et al. 2014). Abiotic factors such as rainfall and flooding are often primary determinants of small mammal assemblages in arid zones (Milstead et al. 2007; Thibault and Brown 2008), but biotic interactions such as predation and competition also play an important role in driving species composition and community assemblage of homeothermic mammals (Johnson et al. 2007; Parsons et al. 2013; Sandom et al. 2013).

Our results suggest biotic interactions are influential in determining the lizard communities of the desert steppe. Although habitat-specific performance in traits such as sprint speed may give one species the competitive advantage it needs to become abundant, and preferences for abiotic factors such as soil type and thermal environment may strongly drive divergence in the lizard community, these abiotic factors together cannot explain lizard community composition in the natural habitat (Table 4). Preferences for biotic factors such as prey type appear to influence species abundance through indirect competition, and behavior such as microhabitat use may influence species abundances through direct interspecific competition. A relatively strong effect of competition would explain the low abundance of *E. argus* in the natural habitat (Table 4). Even with the large scale of our study, however, we cannot determine the strength of influence that each factor had on community composition. We have determined that no single factor explained the community composition fully and thus infer that all of these ecological mechanisms shape how the lizard community responds to habitat alteration.

Habitat alteration can significantly change ecological interactions among terrestrial vertebrates and results in changes in community structure (Henle 1989; Morris et al. 1989; James 1991; Haythornthwaite and Dickman 2006). Our results show why lizard communities diverge at a fine scale within the Mongolian desert steppe, exploiting different abiotic and biotic components of the local environment. Furthermore, these results highlight the importance of conserving plant community composition because it is a strong determinant of many other environmental variables to which organisms respond. In our study, *P. frontalis* and *E. multiocellata* codominated the lizard community in the natural habitat, whereas the structurally dense habitat exhibited a higher abundance of *E. argus*. By contrast, both *Eremias* species had extremely low abundance in the lizard community of the sparse habitat. The sparse habitat also had the highest predation rates across species, suggesting that the sparse habitat may function as a sink for these lizard species. In this desert steppe environment, therefore, management for lizard diversity would benefit from restoration of the sparse habitat to natural habitat and allowance of some dense habitat patches.

Literature Cited

Adolph, S.C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. Ecology 71:315–327.

Arnott, S.E., and M.J. Vanni. 1993. Zooplankton assemblages in fishless bog lakes: Influence of biotic and abiotic factors. Ecology 74:2361–2380.

Attum, O., P. Eason, G. Cobbs, and Baha El Din, S.M. 2006. Response of a desert lizard community to habitat degradation: Do ideas about habitat specialists/generalists hold? Biological Conservation 133:52–62.

Bakken, G.S. 1992. Measurement and application of operative and standard operative temperatures in ecology. American Zoologist 32:194–216.

Case, T.J., and D.T. Bolger. 1991. The role of interspecific competition in the biogeography of island lizards. Trends in Ecology and Evolution 6:135–139.

Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64:1297–1304.

Collins, C.E., J.D. Self, R.A. Anderson, and L.D. McBrayer. 2013. Rock-dwelling lizards exhibit less sensitivity of sprint speed to increases in substrate rugosity. Zoology 116:151–158.

Colloca, F., P. Carpentieri, E. Balestri, and G. Ardizzone. 2010. Food resource partitioning in a Mediterranean demersal fish assemblage: The effect of body size and niche width. Marine Biology 157:565–574.

Cook, C.W., and T.W. Box. 1961. A comparison of the loop and point methods of analyzing vegetation. Journal of Range Management 14:22–27.

Crist, T.O., and J.A. Wiens. 1994. Scale effects of vegetation on forager movement and seed harvesting by ants. Oikos 69:37–46.

Daly, B.G., C.R. Dickman, and M.S. Crowther. 2008. Causes of habitat divergence in two species of agamid lizards in arid central Australia. Ecology 89:65–76.

D'Cruze, N., and S. Kumar. 2011. Effects of anthropogenic activities on lizard communities in northern Madagascar. Animal Conservation 14:542–552.

Dirzo, R., and P.H. Raven. 2003. Global state of biodiversity and loss. Annual Review of Environment and Resources 28:137–167.

Du, W.G., L. Shou, and J.Y. Shen. 2006. Habitat selection in two sympatric Chinese skinks, *Eumeces elegans* and *Sphenomorphus indicus*: Do thermal preferences matter? Canadian Journal of Zoology 84:1300–1306.

Gallucci, F., P. Hutchings, P. Gribben, and G. Fonseca. 2012. Habitat alteration and community-level effects of an invasive ecosystem engineer: A case study along the coast of NSW, Australia. Marine Ecology Progress Series 449:95–108.

Garland, T., Jr., and J.B. Losos. 1994. Ecological morphology of locomotor performance in squamate reptiles. Pp. 240–302 in Ecological Morphology: Integrative Organismal Biology (P.C. Wainwright and S.M. Reilly, eds.). University of Chicago Press, USA.

Goldberg, D.E., and A.M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: A review of field experiments with plants. The American Naturalist 139:771–801.

González-Suárez, M., M. Mugabo, B. Decenciére, S. Perret, D. Claessen, and J.-F. le Galliard. 2011. Disentangling the effects of predator body size and prey density on prey consumption in a lizard. Functional Ecology 25:158–165.

Gotelli, N.J. 2000. Null model analysis of species co-occurrence patterns. Ecology 81:2606–2621.

Gurevitch, J., L.L. Morrow, A. Wallace, and J.S. Walsh. 1992. A meta-analysis of competition in field experiments. The American Naturalist 140:539–572.

Hacking, J., R. Abom, and L. Schwarzkopf. 2014. Why do lizards avoid weeds? Biological Invasions 16:935–947.

Hausdorf, B., and C. Hennig. 2007. Null model tests of clustering of species, negative co-occurrence patterns, and nestedness in meta-communities. Oikos 116:818–828.

Haythornthwaite, A.S., and C.R. Dickman. 2006. Long-distance movements by a small carnivorous marsupial: How *Sminthopsis youngsoni* (Marsupialia: Dasyuridae) uses habitat in an Australian sandridge desert. Journal of Zoology 270:543–549.

Henle, K. 1989. Ecological segregation in an assemblage of diurnal lizards in arid Australia. Acta Oecologica 10:19–35.

Hertz, P.E., R.B. Huey, and R.D. Stevenson. 1993. Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. The American Naturalist 142:796–818.

Higham, T.E., and A.P. Russell. 2010. Divergence in locomotor performance, ecology, and morphology between two sympatric sister species of desert-dwelling gecko. Biological Journal of the Linnean Society 101:860–869.

Huang, D., K. Wang, and W.L. Wu. 2007. Dynamics of soil physical and chemical properties and vegetation succession characteristics during grassland desertification under sheep grazing in an agro-pastoral transition zone in Northern China. Journal of Arid Environments 70:120–136.

Huey, R.B. 1982. Temperature, physiology, and the ecology of reptiles. Pp. 25–91 in Biology of the Reptilia (C. Gans and F.G. Pough, eds.). Academic Press, UK.

Huey, R.B., E.R. Pianka, and T. Schoener. 1983. Lizard Ecology: Studies of a Model Organism. Harvard University Press, USA.

Husak, J.F. 2006. Does survival depend on how fast you *can* run or how fast you *do* run? Functional Ecology 20:1080–1086.

Irschick, D.J., and J.B. Losos. 1999. Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. The American Naturalist 154:293–305.

Jackson, D.A., P.R. Peres-Neto, and J.D. Olden. 2001. What controls who is where in freshwater fish communities: The roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58:157–170.

James, C.D. 1991. Temporal variation in diets and trophic partitioning by coexisting lizards (*Ctenotus*: Scincidae) in central Australia. Oecologia 85:553–561.

Johnson, C.N., J.L. Isaac, and D.O. Fisher. 2007. Rarity of a top predator triggers continent-wide collapse of mammal prey: Dingoes and marsupials in Australia. Proceedings of the Royal Society London Series B 274:341–346.

Lelièvre, H., G. Blouin-Demers, D. Pinaud, H. Lisse, X. Bonnet, and O. Lourdais. 2011. Contrasted thermal preferences translate into divergences in habitat use and realized performance in two sympatric snakes. Journal of Zoology 284:265–275.

Li, F., Y.-S. Kwon, M.-J. Bae, N. Chung, T.-S. Kwon, and Y.-S. Park. 2014. Potential impacts of global warming on the diversity and distribution of stream insects in South Korea. Conservation Biology 28:498–508.

Lisičić, D., S. Drakulić, A. Herrel, D. Dikić, V. Benković, and Z. Tadić. 2012. Effect of competition on habitat utilization in two temperate climate gecko species. Ecological Research 27:551–560.

López, P., and J. Martín. 2013. Effects of microhabitat-dependent predation risk on vigilance during intermittent locomotion in *Psammodromus algirus* lizards. Ethology 119:316–324.

Luiselli, L. 2006. Interspecific relationships between two species of sympatric Afrotropical water snake in relation to a seasonally fluctuating food resource. Journal of Tropical Ecology 22:91–100.

Luiselli, L. 2008. Do lizard communities partition the trophic niche? A worldwide meta-analysis using null models. Oikos 117:321–330.

Manicom, C., and L. Schwarzkopf. 2011. Diet and prey selection of sympatric tropical skinks. Austral Ecology 36:485–496.

McLaughlin, J.F., and J. Roughgarden. 1989. Avian predation on *Anolis* lizards in the Northeastern Caribbean: An inter-island contrast. Ecology 70:617–628.

Miles, D.B. 2004. The race goes to the swift: Fitness consequences of variation in sprint performance in juvenile lizards. Evolutionary Ecology Research 6:63–75.

Milstead, W.B., P.L. Meserve, A. Campanella, M.A. Previtali, D.A. Kelt, and J.R. Gutiérrez. 2007. Spatial ecology of small mammals in north-central Chile: Role of precipitation and refuges. Journal of Mammalogy 88:1532–1538.

Morris, D.W., Z. Abramsky, B.J. Fox, and M.R. Willig. 1989. Patterns in the Structure of Mammalian Communities. Texas Tech University Press, USA.

Nanjing Institute of Soil Science. 1980. Analysis of Soil Physico-Chemical Features. Shanghai Science and Technology Press, China.

Nogueira, C., P.H. Valdujo, and F.G.R. França. 2005. Habitat variation and lizard diversity in a Cerrado area of Central Brazil. Studies on Neotropical Fauna and Environment 40:105–112.

Parsons, E.W.R., J.L. Maron, and T.E. Martin. 2013. Elk herbivory alters small mammal assemblages in high-elevation drainages. Journal of Animal Ecology 82:459–467.

Pawar, S.S., G.S. Rawat, and B.C. Choudhury. 2004. Recovery of frog and lizard communities following primary habitat alteration in Mizoram, Northeast India. BMC Ecology 4:10.

Pelegrin, N., and E.H. Bucher. 2012. Effects of habitat degradation on the lizard assemblage in the Arid Chaco, central Argentina. Journal of Arid Environments 79:13–19.

Petren, K., and T.J. Case. 1998. Habitat structure determines competition intensity and invasion success in gecko lizards. Proceedings of the National Academy of Sciences of the United States of America 95:11739–11744.

Pianka, E.R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4:53–74.

Pianka, E.R. 1976. Competition and niche theory. Pp. 114–141 in Theoretical Ecology: Principles and Applications (R.M. May, ed.). W.B. Saunders Company, USA.

Pianka, E.R. 1986. Ecology and Natural History of Desert Lizards. Princeton University Press, USA.

Pike, D.A., J.K. Webb, and R. Shine. 2011. Removing forest canopy cover restores a reptile assemblage. Ecological Applications 21:274–280.

Pough, F.H. 1989. Organismal performance and Darwinian fitness: Approaches and interpretations. Physiological Zoology 62:199–236.

Qiao, X., G.S. Yang, L. Zhang, P. Xing, and M. Li. 2011. Bird avifauna and community structure in Wuhai, Inner Mongolia. Chinese Journal of Zoology 46:126–136.

Rahel, F.J., and W.A. Hubert. 1991. Fish assemblages and habitat gradients in a Rocky Mountain-Great Plains stream: Biotic zonation and additive patterns of community change. Transactions of the American Fisheries Society 120:319–332.

Roches, S.D., J.M. Robertson, L.J. Harmon, and E.B. Rosenblum. 2011. Ecological release in White Sands lizards. Ecology and Evolution 1:571–578.

Saenz, D. 1996. Dietary overview of *Hemldactylus turctcus* with possible implications of food partitioning. Journal of Herpetology 30:461–166.

Sanderson, J.G. 2004. Null model analysis of communities on gradients. Journal of Biogeography 31:879–883.

Sandom, C., L. Dalby, C. Fløjgaard, W.D. Kissling, J. Lenoir, B. Sandel, K. Trøjelsgaard, R. Ejrnæs, and J.C. Svenning. 2013. Mammal predator and prey species richness are strongly linked at macroscales. Ecology 94:1112–1122.

Schaffler, J.J., J. van Montfrans, C.M. Jones, and R.J. Orth. 2013. Fish species distribution in seagrass habitats of Chesapeake Bay are structured by abiotic and biotic factors. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 5:114–124.

Schoener, T.W. 1983. Field experiments on interspecific competition. The American Naturalist 122:240–285.

Scott, D.M., D. Brown, S. Mahood, B. Denton, A. Silburn, and F. Rakotondraparany. 2006. The impacts of forest clearance on lizard, small mammal and bird communities in the arid spiny forest, southern Madagascar. Biological Conservation 127:72–87.

Selleslagh, J., and R. Amara. 2008. Environmental factors structuring fish composition and assemblages in a small macrotidal estuary (eastern English Channel). Estuarine, Coastal and Shelf Science 79:507–517.

Shenbrot, G.I., K.A. Rogovin, and A.V. Surov. 1991. Comparative analysis of spatial organization of desert lizard communities in Middle Asia and Mexico. Oikos 61:157–168.

Stamps, J.A., and S. Tanaka. 1981. The influence of food and water on growth rates in a tropical lizard (*Anolis aeneus*). Ecology 62:33–44.

Steen, D.A., L.L. Smith, L.M. Conner, A.R. Litt, L. Provencher, J.K. Hiers, S. Pokswinski, and C. Guyer. 2013. Reptile assemblage response to restoration of fire-suppressed longleaf pine sandhills. Ecological Applications 23:148–158.

Sutherland, D.R. 2011. Dietary niche overlap and size partitioning in sympatric varanid lizards. Herpetologica 67:146–153.

Taylor, J.E., and B.J. Fox. 2001. Disturbance effects from fire and mining produce different lizard communities in eastern Australian forests. Austral Ecology 26:193–204.

Thibault, K.M., and J.H. Brown. 2008. Impact of an extreme climatic event on community assembly. Proceedings of the National Academy of Sciences of the United States of America 105:3410–3415.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences of the United States of America 101:10854–10861.

Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W.H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. Science 292:281–284.

Towns, D.R., and G.P. Elliott. 1996. Effects of habitat structure on

distribution and abundance of lizards at Pukerua Bay, Wellington, New Zealand. New Zealand Journal of Ecology 20:191–206.

Tucker, D.B., and L.D. McBrayer. 2012. Overcoming obstacles: The effect of obstacles on locomotor performance and behaviour. Biological Journal of the Linnean Society 107:813–823.

Vitt, L.J., S.S. Sartorius, T.C.S. Avila-Pires, M.C. Espósito, and D.B. Miles. 2000. Niche segregation among sympatric Amazonian teiid lizards. Oecologia 122:410–420.

Wellborn, G.A., D.K. Skelly, and E.E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27:337–363.

Zaady, E., and A. Bouskila. 2002. Lizard burrows association with successional stages of biological soil crusts in an arid sandy region. Journal of Arid Environments 50:235–246.

Zeng, Z.G., J.H. Bi, S.R. Li, S.Y. Chen, D.A. Pike, Y. Gao, and W.G. Du. 2014. Effects of habitat alteration on lizard community and food web structure in a desert steppe ecosystem. Biological Conservation 179:86–92.

Zhao, E.M., K.T. Zhao, and K.Y. Zhou. 1999. Fauna Sinica Reptilia, Volume 2: Squamata. Science Press, China.