

Ecological Trap for Desert Lizards Caused by Anthropogenic Changes in Habitat Structure that Favor Predator Activity

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Abstract: *Anthropogenic habitat perturbation is a major cause of population decline. A standard practice managers use to protect populations is to leave portions of natural habitat intact. We describe a case study in which, despite the use of this practice, the critically endangered lizard *Acanthodactylus beershebensis* was locally extirpated from both manipulated and natural patches within a mosaic landscape of an afforestation project. We hypothesized that increased structural complexity in planted patches favors avian predator activity and makes these patches less suitable for lizards due to a heightened risk of predation. Spatial rarity of natural perches (e.g., trees) in arid scrublands may hinder the ability of desert lizards to associate perches with low-quality habitat, turning planted patches into ecological traps for such species. We erected artificial trees in a structurally simple arid habitat (similar to the way trees were planted in the afforestation project) and compared lizard population dynamics in plots with these structures and without. Survival of lizards in the plots with artificial trees was lower than survival in plots without artificial trees. Hatchlings dispersed into plots with artificial trees in a manner that indicated they perceived the quality of these plots as similar to the surrounding, unmanipulated landscape. Our results showed that local anthropogenic changes in habitat structure that seem relatively harmless may have a considerable negative effect beyond the immediate area of the perturbation because the disturbed habitat may become an ecological trap.*

Keywords: *Acanthodactylus beershebensis*, afforestation, dispersal, habitat selection, population decline, shrike, structural complexity, survival

Creación de una Trampa Ecológica para Lagartijas de Desierto con la Adición de una Estructura de Hábitat que Favorece la Actividad de Depredadores

Resumen: *La perturbación antropogénica de hábitat es una causa mayor de la declinación de poblaciones. Una práctica estándar que utilizan los manejadores para proteger poblaciones es dejar intacto porciones de hábitat natural. Describimos un estudio de caso en el que, no obstante el uso de esta práctica, la lagartija *Acanthodactylus beershebensis*, en peligro crítico, fue extirpada localmente tanto de parches manipulados como naturales en un mosaico paisajístico de un proyecto de reforestación. Nuestra hipótesis fue que el incremento en la complejidad estructural en parches sembrados favorece la actividad de aves depredadoras y hace que estos parches sean menos favorables para lagartijas debido a un alto riesgo de depredación. La rareza espacial de perchas naturales (e.g., árboles) en matorrales áridos puede limitar la habilidad de las lagartijas de desierto para asociar las perchas con hábitat de baja calidad, y los árboles sembrados pueden crear trampas ecológicas para tales especies. Erigimos árboles artificiales en un hábitat árido estructuralmente simple (similar a la manera en los árboles fueron sembrados en el proyecto de reforestación) y comparamos la dinámica de las poblaciones de lagartijas en parcelas con y sin estas estructuras. La supervivencia de*

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lagartijas en las parcelas con árboles artificiales fue menor que la supervivencia en parcelas sin árboles artificiales. Los juveniles se dispersaron hacia parcelas con árboles artificiales en una forma que indicó que percibieron que la calidad del área era similar al paisaje circundante no manipulado. Nuestros resultados mostraron que los cambios antropogénicos locales en la estructura del hábitat que parecen relativamente inocuos pueden tener un considerable efecto negativo más allá del área inmediata de la perturbación porque el hábitat perturbado puede convertirse en una trampa ecológica.

Palabras Clave: *Acanthodactylus beershebensis*, alcaudón, complejidad estructural, declinación poblacional, dispersión, selección de hábitat, reforestación, supervivencia

Introduction

Habitat perturbation due to human alteration of landscapes is a major cause of population declines. To circumvent such declines, managers often protect some fraction of natural habitat deemed to be of sufficient size to maintain viable populations within a larger, developed land matrix. Such seemingly intuitive and straightforward conservation measures may fail to stem population decline because they fail to consider how altered land-use changes species' movement behavior and interactions with other species within and outside the protected area. Thus, despite efforts to protect habitat, the nature of land use outside protected areas can draw species away from protected areas and create ecological traps (Schlaepfer et al. 2002). Ecological traps are problematic because they lead to species population decline in both the disturbed and protected habitat. Such situations could lead policy makers to conclude that human alteration of land cannot be the cause of species declines because similar declines are observed in the protected areas.

Ecological Traps

Ecological traps are low-quality habitats that are preferred by animals over adjacent, better habitats (Dwernychuk & Boag 1972; Gates & Gysel 1978; Kristan 2003). In general, the existence of such traps is not expected given that natural selection should favor animals that are capable of using environmental elements (i.e., traditional cues) to reliably assess habitat quality and to choose habitats that maximize their fitness (Rosenzweig 1981). Partially on the basis of these assumptions, the theory of source-sink dynamics (Pulliam 1988) predicts that source populations should not be degraded by the poor-quality sink habitats (Dias 1996). Nevertheless, the rate at which anthropogenic activities alter habitat structure typically exceeds that of animals' evolutionary capacity to respond to change. Addition of novel elements that mimic attractive habitat cues, changes in intensity, type, or number of settlement cues that are normally used by individuals (Horvath et al. 1998; Kriska et al. 1998; Weldon & Haddad 2005), and degradation of habitat quality that is not associated with perceivable changes in settlement cues normally used by an individual (e.g., Lloyd

& Martin 2005) can generate ecological-trap dynamics. The underlying mechanism for all of these scenarios is a mismatch between traditionally attractive cues and the actual quality of the habitat. This mismatch can lead to animals preferring low-quality habitats over adjacent better habitats (Kokko & Sutherland 2001) and thereby cause individuals, normally residing in source habitats, to occupy poor-quality habitat (Gundersen et al. 2002).

We examined another scenario that may create ecological-trap dynamics: addition of structural elements associated with predation (i.e., repulsive cues) that are naturally rare (e.g., perch sites). Because an ecological trap erodes the source habitat and may cause species extinctions, identifying the management scenarios that generate ecological-trap dynamics is important.

Acanthodactylus beershebensis

The lizard *Acanthodactylus beershebensis* is endemic to loess scrublands of the northern Negev desert, Israel (Moravec et al. 1999). Severe population declines in the late-20th century led to the species being listed as critically endangered. Prior to its listing, portions of the species' relict habitats were manipulated by the Forestry Department of the Jewish National Fund (JNF) as part of the Savannization Project. The project's goal was to increase plant biomass and species richness by reducing resource (e.g., water, soil, and nutrients) leakage from the ecosystem. A series of longitudinal pits and dykes along the contour line of the slopes (i.e., contour catchments) were constructed (Eldridge et al. 2002). The pits accumulate runoff and nutrients and are used to support planted trees (Shachak et al. 1998). Within the project boundaries, managers created a mosaic of natural and altered habitat patches. *Acanthodactylus beershebensis* disappeared from both natural and altered habitats within the project boundaries in less than 11 years after the natural habitat was disturbed (Hawlena & Bouskila 2006). Land managers argued that because *A. beershebensis* disappeared from both natural and altered habitats, the lizard's disappearance could not have been caused by the afforestation project. Because of this apparent lack of causality between impact and species loss, the project was slated for expansion to other locations.

Hawlena and Bouskila (2006) propose that the creation of an ecological trap explains the extirpation of

A. beershebensis' in the area managed under the Savannization Project. They hypothesize that planting trees in perch-less habitats increases the abundance of avian predators and their hunting efficiency. This in turn makes the manipulated habitat less suitable for lizards owing to the heightened risk of predation. Prey should be capable of using structural elements to assess the risk of predation (Stamps 2001), even if predator activity is not evident during the time habitat-selection decisions are made (e.g., Bouskila 1995). Nevertheless, spatial rarity of natural perches (e.g., trees, dry inflorescence stems, bushes) and human-made perches (e.g., poles, shrub piles) in arid scrublands may hinder the ability of desert lizards to associate perches with low-habitat quality. Thus, a rapid increase in the number of available perches could lead to the perception by prey that a managed habitat is as risky as a natural habitat, generating an equal-preference ecological trap. Numerous anthropogenic activities generate subtle changes in habitat complexity (e.g., electric lines, fence lines, road sign poles, invasive plants) that can alter predator-prey interaction. Empirical examination of whether such common human-induced habitat modifications can generate ecological-trap dynamics is essential to protect declining populations.

We examined our hypothesis by adding small groups of artificial trees to homogenous scrubland. This emulated the afforestation practices (Savannization) used by the JNF and provided perches for the lizards' main predators in this area, the Southern Gray Shrike (*Lanius meridionalis*) and the Common Kestrel (*Falco tinnunculus*) (Hawlena & Pérez-Mellado 2009). To determine that our structural manipulation created ecological traps (following the definitions of Robertson and Hutto (2006), we tested whether the manipulated subplots were of considerably poorer quality for lizards, but were at least as attractive as the adjacent patches that were otherwise similar to the manipulated patches.

Methods

Study System

We conducted the field experiment in a loess scrubland in the northern Negev Desert, Israel (N 31° 14', E 34° 38'). The scrubland, dominated by a small woody perennial shrub *Noea mucronata*, was structurally simple with very few natural or human-made perches from which predatory birds could hunt. Our focal species *A. beershebensis* is the most abundant lizard in this habitat. All *A. beershebensis* hatch synchronously in <3 weeks, beginning in the late May. Hatchlings have a unique striped body and blue tail coloration that changes to a blotched pattern and brown tail 3 weeks after hatching. This characteristic simplifies identification of hatching

dates (Hawlena et al. 2006). During the first month of their life, hatchlings disperse hundreds of meters from their natal sites, but later they remain loyal to small home ranges. Mating occurs in February, and most females lay eggs until mid-April. Most adults die by the end of April, and there is no overlap between cohorts.

Experimental Design

We selected five plots of homogenous habitat at least 300 m from each other. The home range of *A. beershebensis* is small (mean [SE] = 607 m² [85], $n = 20$; i.e., a 24- to 32-m diameter for a circular home range; D.H., unpublished data). Thus, the five plots were independent replicates. In each of the chosen locations, we set up two 80 × 80 m subplots separated by a 30-m buffer. Although the buffer was narrow, we captured only five lizards in neighboring subplots after natal dispersal and establishment of home ranges. In one randomly selected subplot of each pair, we erected 16, 1.5-m metal poles to attract avian predators. The paired subplot served as a control. We attached barbed wire to a 50 × 50 cm metal frame at the top of the poles to mimic thorny branches, creating suitable locations for shrikes to perch and impale their prey. The direct impact of perching predators in our site is limited to <30 m from a perch (Hawlena and Bouskila 2006). Thus, predators in the manipulated subplots were not expected to increase the risk of predation considerably in the control subplots.

We observed each plot for 2 h and calculated the time shrikes were present in each subplot as the average of three observations. Shrikes spent significantly more time in manipulated subplots (mean [SE] = 17.9% [2.5] of total survey time) than in control subplots (2.2% [0.8]) (Hawlena & Bouskila 2006). Other than their physical presence, the artificial trees did not alter any other components of the habitat (e.g., shade, food, or shelter) that could be perceived by lizards as attractive cues (e.g., Shochat et al. 2005).

In each subplot we buried 64 pitfall traps (10-L buckets buried flush with the ground) spaced 10 m apart. In this way, we were able to trap lizards in a random fashion and to sample all subplots simultaneously. We trapped lizards for three consecutive days each month from September 1999 (1 month after adding the perches) until September 2001. We supplemented one trapping session during June, decreasing the first two intervals between trapping sessions to 2 weeks. We marked all lizards individually and measured their snout-vent length (SVL) with a transparent ruler to the nearest 1 mm and their weight to the nearest 0.1 g with an electronic field scale. We released all lizards at the location of capture within 24 h. To prevent animal heat stress during trapping, we checked the traps at least once every 2 h. Between trapping periods, the pitfalls were closed tightly.

Data Analyses

We used program MARK (White & Burnham 1999) to estimate survival and recapture probability. We used data from a single cohort from the time of hatching until females laid eggs (May 2000 until late March 2001). There were 12 trapping sessions. In the analyses, the first two sessions received half the weight of the other sessions. In total, we captured 368 lizards of which 258 were different individuals. We used Cormack-Jolly-Seber (CJS) models for open populations to estimate temporal variation in apparent survival (Φ) (which may include dispersal and recapture rates) (Seber 1986). To test the effect of increased perch availability (predation pressure) on lizard survival rate and the probability of recapture, we compared models with various combinations of treatment and plot (block) effects. To reveal whether the effect varied during ontogeny, we also tested for variation in survival and recapture rate over time. Specifically, we tested for variation soon after hatching (May-June); in August when lizard activity is restricted to short periods of daily activity; and in February when lizards are engaged in mating activities. While trapping we noticed that recapture probability in one subplot (4 control) appeared to be much lower than in the rest of the plots, possibly because it was placed on a moderate slope. To improve our survival estimations we included models in which subplot 4 control had a unique trapping parameter. We used Akaike's information criterion corrected for small sample size (AIC_c) for model comparison (Burnham & Anderson 2002).

We could not use closed-population models to estimate lizard density because the probability of recapture during a single trapping session (i.e., within a 3-day period) was too small. Thus, we used the minimal number alive (MNA) as our index for lizard density and density-related measures. We used a two-way repeated measures analysis of variance (ANOVA) to compare hatchling (soon after hatching) and juvenile (soon after lizards settled in their post dispersal home ranges) densities between manipulated and control subplots. We removed interaction terms with p values >0.2 from the analyses. To rule out the possibility that an increase in juvenile numbers following the dispersal event in the manipulated subplots resulted from late hatching, we used a chi-square test to compare the late-June ratios of blue-tailed juveniles between control and manipulated subplots.

Immigrants in a good condition are more likely to settle in high-quality habitats (Stamps 2001). Thus, differences in immigrant phenotype may provide additional evidence on how lizards perceived habitat quality. We treated all juveniles trapped during late June and not captured previously as immigrants and used a mixed model ANOVA to test for size (SVL) differences in captured lizards between the two treatments. We used mixed-model analysis of covariance to test for differences in immigrant's

body condition. We used lizard mass as the dependent variable and SVL as a covariate. Our data set probably included a small number of individuals that hatched in our plots but had not been captured previously. Their inclusion in analyses of immigrant phenotype calls for a more-conservative interpretation of our results because individuals that hatched in the manipulated subplots were on average smaller than their conspecifics from the control subplots (D.H., unpublished data).

We elucidated temporal patterns of patch dynamics by calculating the differences between lizard density within each subplot between every two consecutive trapping sessions and dividing the differences by the sum of the two densities (to standardize the results). We averaged the normalized differences in the five manipulated subplots and repeated the same procedure for the five control subplots. For all analyses, significance tests were two tailed at $\alpha = 0.05$.

Results

All leading models ($\Delta AIC_c < 2.0$ - Burnham & Anderson 2002) included our treatment (Table 1). Survival estimation, until the reproduction season, for manipulated subplots ($\Phi = 0.09$) was about half that in control subplots ($\Phi = 0.21$). Comparison of initial hatchling density (early June) between manipulated (mean [SE] = 5.5 lizards per subplot [SE 1.6]) and control subplots (12.3 [SE 2.2]) revealed that hatchlings were significantly less abundant in the manipulated subplots (treatment: $F = 43.4$, $df = 1, 4$, $p = 0.003$; year: $F = 0.2$, $df = 1, 4$, $p = 0.7$; Fig. 1). A similar comparison of post dispersal densities (July) failed to reject our null hypothesis of no differences between manipulated (mean [SE] = 6.8 lizards per subplot [SE 0.8]) and control (6.5 [SE 1.2]) subplots (treatment: $F = 0.073$, $df = 1, 4$, $p = 0.801$; year: $F = 18.692$, $df = 1, 4$, $p = 0.01$).

We failed to reject the null hypothesis of no differences in the ratios of blue-tailed hatchlings between manipulated and control plots (late June of 2000: $\chi^2 = 1.1$, $df = 1$, $p = 0.29$; and late June of 2001: $\chi^2 = 0.1$, $df = 1$, $p = 0.75$). By July all trapped juveniles in both treatments had adult coloration and pattern (i.e., no blue-tailed morphs were trapped). We failed to reject the null hypotheses of no differences in immigrants' SVL ($F = 0.027$; $df = 1, 23.71$, $p = 0.87$) or immigrants' body condition ($F = 0.185$; $df = 1, 5.2$, $p = 0.685$) between the manipulated and control subplots. Nevertheless, we rejected the null hypothesis of no difference in immigrants' SVL between the different plots ($F = 5.27$, $df = 4, 16.42$, $p = 0.006$). During June, the number of hatchlings markedly increased in the manipulated subplots, whereas we found no increase during the same period in the control subplots (Fig. 1). Density reduction occurred during July 2001 in

Table 1. Competing models for estimation of recapture and survival probabilities of *A. beershebenensis* sorted by their Akaike's information criterion corrected for small sample size (AIC_c).

Parameter no.	Model likelihood	Delta AIC_c	AIC_c	Model parameters*
8	1.00	0	766.82	$\Phi(\text{treat} \times t_{[MJ,F]}), p(t_{[A,F]} \times 4c)$
7	0.810	0.41	767.24	$\Phi(\text{treat} \times t_{[F]}), p(t_{[A,F]} \times 4c)$
9	0.4035	1.82	768.64	$\Phi(\text{treat} \times t_{[MJ,F]}), p(\text{treat} \times t_{[A,F]} \times 4c)$
6	0.386	1.90	768.72	$\Phi(\text{treat}), p(t_{[A,F]} \times 4c)$
7	0.32	2.27	769.08	$\Phi(\text{treat} \times t_{[MJ]}), p(t_{[A,F]} \times 4c)$
7	0.2571	2.72	769.54	$\Phi(\text{treat} \times t_{[MJ,F]}), p(t_{[A,F]})$
7	0.2461	2.81	769.63	$\Phi(t_{[MJ,F]}), p(t_{[A,F]} \times 4c)$
12	0.2208	3.02	769.84	$\Phi(\text{treat} \times \text{block} \times t_{[MJ,F]}), p(t_{[A,F]} \times 4c)$
11	0.1773	3.46	770.3	$\Phi(\text{block} \times t_{[MJ,F]}), p(t_{[A,F]} \times 4c)$
5	0.1298	4.09	770.91	$\Phi(\text{treat}), p(t_{[A,F]})$
5	0.116	4.317	771.14	$\Phi(\cdot), p(t_{[A,F]} \times 4c)$
4	0.0614	5.58	772.40	$\Phi(\cdot), p(t_{[A,F]})$
3	0.0023	12.18	779.00	$\Phi(\text{treat}), p(\cdot)$
2	0.0011	13.71	780.53	$\Phi(\cdot), p(\cdot)$

*Key: p, recapture probability; Φ , survival probability; (\cdot), constant; t, effect of time (MJ, May-June; A, August; F, February); treat, effect of treatment; c, xxx.

the control subplots, whereas lizard numbers increased in the manipulated subplots. In both years, the increase in hatchling numbers within the manipulated subplots was in spite of lower survival in those subplots.

Discussion

Our results showed that artificial structures that favored predator activity generated ecological traps for the critically endangered lizard *A. beershebenensis*. To be an ecological trap, low-quality patches must be perceived by an animal as being at least as good as the surrounding higher quality patches (Robertson & Hutto 2006). *Acanthodactylus beershebenensis* had lower survival rates in all manipulated subplots that was not compensated for by increased recruitment (i.e., overall lower hatchling numbers in all manipulated subplots soon after hatch-

ing). Survival estimates were lower in the manipulated subplots even in June and July, when lizard numbers in the manipulated subplots were increasing and survival would be underestimated in the control subplots due to emigration. Hence, we conclude that supplementation of perches turned the manipulated subplots into low-quality patches for *A. beershebenensis*.

Density-dependent dispersal to habitats characterized by high periodic mortality can generate ecological-trap dynamics (Gundersen et al. 2001). By the end of the dispersal season, we did not find differences in lizard densities between the manipulated and control subplots, which may indicate there was density-dependent dispersal into the manipulated subplots. Relative abundance cannot be considered a sole surrogate measure for habitat preference, and other correlated lines of evidence are needed to improve the certainty that the preference is accurately assessed (Robertson & Hutto 2006). Because we did not find differences in the ratios of blue-tailed juveniles or in the SVL between the control and manipulated subplots, and because we trapped no blue-tailed morphs in July, late hatching does not explain the density equalization between the paired subplots.

This leaves only dispersal as a possible mechanism for this equalization (Lecomte et al. 2004) and indicates that either *A. beershebenensis* was unable to correctly assess the quality of the patches (in terms of predation threat) or was forced to settle in these patches because of competition. The latter process, known as ideal despotic distribution (IDD), assumes that highly competitive immigrants will settle in high-quality habitats and force less-competitive immigrants to settle in poor-quality habitat (Fretwell 1972). Large hatchlings or hatchlings with good body condition are better competitors than smaller hatchlings or hatchlings of poorer body condition (Fox 1978; Olsson & Shine 1997; Warner & Andrews 2002). Thus,

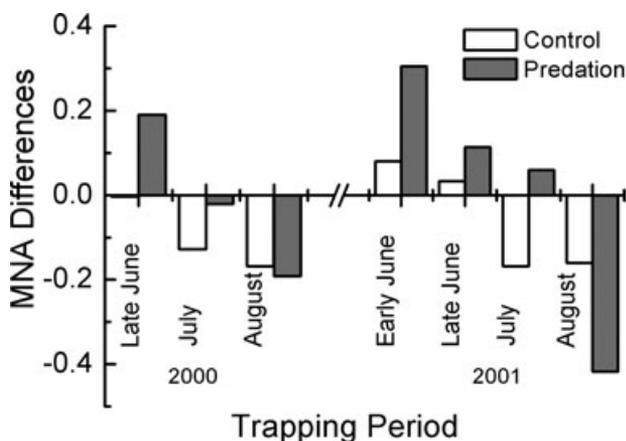


Figure 1. Average difference in density of *A. beershebenensis* between consecutive trapping sessions.

if IDD were the cause of the density equalization process, then one would expect to find larger individuals or individuals with better body condition in the more-suitable control subplots. Our findings on SVL and body condition of juveniles do not support this. Because we found no differences in SVL between the treatments, we conclude that dispersing lizards cannot assess differences in habitat quality induced by our manipulation. Hence, despite ample visual cues (i.e., perches) of poor quality, lizards dispersed into the manipulated subplots as though they were of similar quality to the control subplots: the manipulated patches were equal preference ecological traps.

Others have considered the inability of prey to assess changes in predator activity as a prominent cause of ecological traps (Schlaepfer et al. 2002). In this sense, our current study is not unique. Nevertheless, unlike those studies in which anthropogenic activities altered several habitat components simultaneously and the modifications attracted both predators and their prey (e.g., Weldon & Haddad 2005), we manipulated only one (physical) component of the habitat—number of perches for the predator—and did not provide attractants to the prey. This raises the question, why have lizards not evolved to assess structural changes that are associated with elevated activity of native predators as repulsive habitat cues?

Animals use indirect cues (e.g., structural elements) to evaluate habitat quality (Bouskila & Blumstein 1992; Stamps 2001). Such an indirect assessment process can evolve only if selection against individuals that fail to associate environmental cues with the intrinsic habitat quality considerably affects population demography (Battin 2004). *Acanthodactylus beershebensis* is endemic to the loess scrubland of the northern Negev desert. Sparse clusters of natural and human-made perches characterized this habitat for the last approximately 7000 years (Finkelstein & Perevolotsky 1990). Therefore, most lizards are not exposed to avian predators that ambush from perches. We hypothesize that *A. beershebensis* is not adapted to identify possible perches as cues for increased predation because such local adaptation is constantly flooded by gene flow from the entire population that is not selected to interpret possible perches as a cue for predation. These insights call into question the utility of using optimal habitat selection theory to guide thinking about animal habitat choice when animals must evaluate the quality of a rare or infrequently encountered habitat.

Conservation Implications

Local anthropogenic perturbations with apparently low environmental impact may exert a considerable influence beyond the immediate area of the perturbation by turning the manipulated area into an ecological trap. Ecological-

trap dynamics may be an indirect result of the perturbation and thus may not be noticed readily. Specifically in our example, modification of habitat structure did not affect the lizards directly; it merely changed the spatial activity of predators native to this community. Such situations may be relatively common (e.g., along power lines, roads with many signposts, fences). We argue that not all species are similarly vulnerable to such structural modification and that the species' evolutionary history determines its vulnerability. Specialist species inhabiting a structurally simple habitat may lack the ability to identify and respond to biotic consequences of novel structural attributes, which makes these species more vulnerable to structural habitat modifications than generalist species or species from structurally complex habitats.

We demonstrate that local estimates of population density alone cannot be used to assess the conservation status of a population. Other information, such as survival estimates, spatial dynamics, and natural-history data, is needed. Our study's conceptual and applied consequences highlight the value of applying evolutionary and community ecology concepts as part of an active management strategy. Without such an integrative approach, long and expensive conservation efforts could be ineffective and could undermine the scientific integrity of conservation biology. Moreover, we provide an example of the mutual benefit conservation efforts and fundamental ecology could realize by designing ecological experiments with focal conservation problems in mind.

Our study provides an explanation for the disappearance of *A. beershebensis* from the mosaic landscape of the Savannization project. We used the results of our experiment to convince the JNF and other land-management agencies to abandon the Savannization plans for the remaining *A. beershebensis* habitats and to support establishment of a large sanctuary surrounded by sufficient buffer zones to protect the lizard and other species specialized in loess scrublands.

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