Lizard community structure across a grassland – creosote bush ecotone in the Chihuahuan Desert

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Abstract: I investigated the distribution and abundance of lizard species (*Aspidoscelis inornatus*, *Aspidoscelis tesselatus*, *Aspidoscelis tigris*, *Aspidoscelis uniparens*, *Cophosaurus texanus*, *Crotaphytus collaris*, *Eumeces obsoletus*, *Gambelia wislizenii*, *Holbrookia maculata*, *Phrynosoma cornutum*, *Sceloporus magister*, and *Uta stansburiana*) across a desert grassland – creosote bush (*Larrea tridentata*) ecotone in Dona Ana County, New Mexico. The ecotonal area in the Jornada del Muerto basin has increased dramatically in the past 150 years because of the rapid spread of creosote bush. I asked four related questions: how large and where is the ecotone based on vegetative structure, and do lizard abundance and diversity change across the ecotone? Vegetation data were analyzed using discriminate function analysis to determine the extent of the ecotone. Changes in lizard abundance across the ecotone were analyzed by analysis of variance. During two summers, 677 individual lizards of 9 genera and 12 species were captured. Lizard abundance increased with increasing distance from the ecotone and was similar in grassland and creosote bush habitat. Grasslands had higher species richness than both the creosote bush and ecotone habitats. Grassland sites had greater habitat heterogeneity than did creosote bush sites. No ecotone specialist species were detected, and all common lizard species could be found in each habitat. Three potential explanations for decreased abundance in the ecotone are presented: (1) increased risk of predation, (2) decreased prey abundance, and (3) lack of species-specific microhabitat requisites.

Résumé : J'ai étudié la distribution et l'abondance des lézards (*Aspidoscelis inornatu*s, *Aspidoscelis tesselatus*, *Aspidoscelis tigris*, *Aspidoscelis uniparens*, *Cophosaurus texanus*, *Crotaphytus collaris*, *Eumeces obsoletus*, *Gambelia wislizenii*, *Holbrookia maculata*, *Phrynosoma cornutum*, *Sceloporus magister* and *Uta stansburiana*) à travers un écotone prairie désertique – maquis à larée tridentée (*Larea tridentate*) dans le comté de Dona Ana au Nouveau-Mexique. La surface de cet écotone dans la vallée de la Jornada del Muerto s'est accrue considérablement au cours des 150 dernières années à cause de l'envahissement rapide de la larée tridentée. Quatre questions interdépendantes ont été posées : Quelle est la taille de l'écotone? Où est-il localisé? (Ces deux questions ont été abordées d'après la structure de la végétation.) Est-ce que l'abondance et la diversité des lézards varient à travers l'écotone? Les données de végétation ont été soumises à une analyse factorielle discriminante afin de déterminer l'étendue de l'écotone. Les changements de l'abondance des lézards ont été soumis à une analyse de variance. Durant deux étés, 677 lézards appartenant à 9 genres et 12 espèces ont été capturés. L'abondance des lézards augmente quand on s'éloigne de l'écotone et elle est semblable dans les habitats de prairie et de maquis. La richesse en espèces est plus grande dans les prairies que dans les habitats de maquis et d'écotone. Les sites de prairie possèdent une hétérogénéité d'habitats supérieure à celle des sites de maquis. Il n'existe pas d'espèce spécialiste des écotones et toutes les espèces communes de lézards se retrouvent dans chacun des habitats. L'abondance réduite des lézards dans l'écotone peut être expliquée par (1) le risque accru de prédation, (2) la faible abondance des proies et (3) l'absence de caractéristiques du microhabitat nécessaires pour ces espèces.

[Traduit par la Rédaction]

Introduction

In the Chihuahuan Desert, large areas of desert grassland have been rapidly invaded by xeric adapted native shrubs (Buffington and Herbel 1965; Gibbens and Beck 1988). The desert grassland – creosote bush (*Larrea tridentata*) contact is a natural ecotone with a long historical record in the Chihuahuan Desert. In the Jornada del Muerto basin, creosote bush was formerly limited to gravel ridges; invasion of the grassland of the Jornada basin is a relatively recent event. In 1858, creosote bush was not found in basin grassland sites, but by 1963, approximately 15% of all basin grassland sites had become dominated by creosote bush (Buffington and Herbel 1965). Overgrazing by cattle, climate change, and fire suppression are all implicated as causes for this habitat shift (Buffington and Herbel 1965; Gibbens and Beck 1988).

Animal community responses may often parallel vegetative patterns found at ecotones because of the effect of dominant plants on ecosystem function and habitat structure (Risser 1993). Ecotones are defined both spatially and temporally with effects differing on those two dimensions (Gosz 1993). The edge caused by the transition between habitats may be critical to ecosystem and landscape function. Harris

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(1988) defined several environmental effects associated with anthropogenic edges, such as invasion of exotic species, increased habitat diversity, and altered microclimate (changes in insolation, wind, water flux, and temperature). Changes in abiotic factors across an ecotone can alter nutrient transport and deposition between adjacent habitats (Johnston 1993). Such changes can profoundly influence animal community structure, patterns of abundance, and species diversity (Harris 1984; Murcia 1995; Fagan et al. 1999).

Habitat edge effects on lizard communities have been little studied. Most studies of desert lizard communities, such as Barbault and Maury (1981), define habitats in which lizards are found without addressing any factors relating to the habitat edges. Some tropical lizards are gap specialists that depend on increased microhabitat temperatures typical of these habitat edges (Sartorius et al. 1999). Schlaepfer and Gavin (2001) found that lizard abundance changed in edge habitat with a change from rainy to dry seasons. A recent study in Australia (Conroy 1999) attempted to determine how lizards respond to tropical edges. He found no difference in lizard community structure across an ecotone between dry and wet tropical forests. Studies of ecotones and edge effects on desert lizard communities are almost nonexistent.

In this study, I analyzed lizard community structure along a desert grassland – creosote bush ecotone. I ask several related questions: (*i*) what is the width of the ecotone, (*ii*) how is it distinct from the grassland and creosote habitats, (*iii*) do lizard abundance and diversity change across the ecotone? This study has implications for how communities are altered in a rapidly changing environment. Desert lizards are ideal models for studies of desert edge effects because they are abundant, diverse, mostly diurnal, do not migrate, are important to desert food webs as predators on invertebrates and small vertebrates, and are prey for a diversity of vertebrates, particularly birds and snakes (Pianka 1986).

Materials and methods

Study area

This study was conducted on the Chihuahuan Desert Rangeland Research Center (1360 m; 32°N, 106°W) located in the Jornada del Muerto basin. The Research Center is a 25 900-ha portion of the Jornada Long-Term Ecological Research site (http://jornada.nmsu.edu).

Transects were established on the eastern piedmont and basin slopes of the Mount Summerford bajada, part of the Dona Ana Mountains. Four replicate transects were visually selected to each contain an abrupt vegetative shift from grassland to creosote bush (Fig. 1). Each transect was 246 m long. All transects were located on the eastern bajada slope of Mount Summerford. Two transects were on the upper piedmont slope, one transect was placed on the lower piedmont slope, and the last transect was established on the upper basin slope. For descriptions of the vegetation of the bajada slope, see Wierenga et al. (1987) and Wondzell et al. (1996).

Data collection

Lizards were captured in pitfall traps made of No. 10 coffee cans stacked two deep. Transects were composed of 11 cross-shaped drift-fence trapping arrays 6 m in diameter connected by silt fencing with five pitfalls, one at each end and in the middle. A clay tile covered each pitfall trap to minimize heat stress to trapped animals. Transects were oriented perpendicular to the grassland – creosote bush ecotone with one array at the center of the ecotone (0 m) and two arrays extending logarithmically into each habitat at ±9, ±21, ±39, ±69, and ±123 m giving a total of 11 arrays per transect. Traps were arranged logarithmically to concentrate trapping effort near the edge. This allowed estimation of the scale at which the lizard community distinguished the ecotone from the grassland and creosote bush habitats. In summer 2000, three of the four transects were established, two on the upper and one on the lower piedmont slope. Traps were open 27 May – 4 June and 25 June – 4 August. One additional transect was established on the upper basin slope in 2001 and all four transects were open 21 May – 24 July and 3–7 August. Traps were checked every day between 0700 and 1400 to reduce lizard mortality. Each captured lizard was marked by toe clipping.

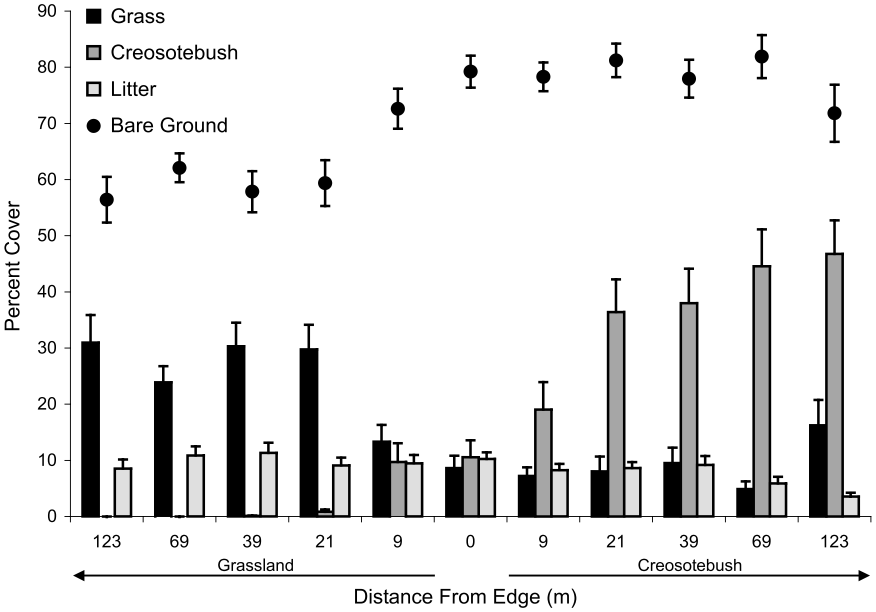
Fig. 1. Grassland – creosote bush (*Larrea tridentata*) ecotone on the Mount Summerford bajada.

Vegetative cover was measured inside six 1-m^2 plots at each trap array. Plots were established at three randomly chosen distances on each side of the array parallel to the edge. A 1-m^2 PVC grid subdivided into 100 equal sections was placed on the ground. Within each grid, percent cover was estimated for six categories: bare soil, litter, grass, creosote, yucca, and other shrubs. Percent cover could be greater than 100%, owing to overlapping canopy cover of shrubs (Huenneke et al. 2001).

Analyses

I used discriminate function analysis (DFA) to determine the spatial extent of the ecotone with respect to vegetative structure (SPSS version 10.0) (SPSS Inc. 1999). I used DFA rather than spatial analyses because my plots were logarithmically spaced (see Fortin et al. 2000). DFA was used to discriminate between the 11 replicated trap arrays established across the ecotone. New functions created by DFA are linear combinations of the original variables, which maximize between-group variance and indicate the variables that contribute most to group separation. All habitat parameters

Fig. 2. Habitat characteristics with increasing distance from the ecotone. Measurements are percent coverage with the potential to have greater than 100%, owing to canopy coverage. All values are means ± 1 SE.



were included and arcsine square-root transformed (Sokal and Rohlf 1995).

Lizard abundance data were analyzed by two-way analysis of variance (ANOVA). Habitat (grass, creosote bush, and ecotone) and lizard species (*Aspidoscelis tesselatus*, *Aspidoscelis tigris*, *Aspidoscelis uniparens*, *Eumeces obsoletus*, *Phrynosoma cornutum*, *Sceloporus magister*, and *Uta stansburiana*) were used to predict changes in lizard abundance in the different habitats. Abundance was entered as number of individuals captured per trap-day and averaged across the distances in each habitat as determined by the DFA. Rare species were defined as those having less than five individuals captured or those that were captured in only one year; these species were excluded from analyses. Significant main effects from the model were compared using the Tukey–Kramer HSD multiple comparison procedure. One-way ANOVAs were used to determine habitat preferences for each individual species. Rate and directions of change in lizard abundance with increasing distance from the edge were analyzed by quadratic contrast. All analyses were performed using JMP version 4.0.4 (SAS Institute Inc. 2001). Only first-capture information was used in all analyses; recaptures were ignored because of trapping biases.

Species accumulation curves are used to demonstrate trends in diversity in different habitats. The species accumulation curves were created for each habitat using trap nights as the sampling effort, and the order was randomized 50 times using EstimateS software (Colwell 1997). Species accumulation curves allow for direct comparisons between studies without the conceptual and semantic problems inherent in diversity indices (Hurlbert 1971; Moreno and Halffter 2000).

Results

All three habitat types had distinct vegetative profiles. Creosote bush sites were dominated by creosote bush with few to no other shrubs and an abundance of bare soil. Larger creosote bush shrubs often had small patches of grass at their bases as well as packrat (*Neotoma* spp.) nests. Grassland sites were dominated by large grass clumps interspersed with smaller areas of bare soil, scattered small shrubs, and yuccas. The ecotone is a transition between the two habitats with fewer and smaller clumps of grass, a mix of small creosote bush and other shrubs, no overlapping canopy, and large areas of bare soil (Fig. 2).

The DFA ordination of distance from ecotone separates the three habitats (Fig. 3). The first two discriminate functions accounted for 94.3% of the variation described. Discriminate function 1 is significant, accounting for 86.9% of the variation, and described a gradient based on creosote bush cover. Discriminate function 2 is nonsignificant, accounting for only 7.4% of the variation. Creosote bush coverage significantly separated each group's mean centroid. Function 2 was positively correlated with percent coverage of grass and negatively correlated with percent coverage of litter and bare soil (Table 1). Three habitat types are distinct on function 1 of the DFA. A tight cluster of grassland sites occurs 21–123 m from the ecotone. A cluster of three ecotonal sites includes the trap arrays located 9 m on either side of the edge. The remaining cluster, 21–123 m from the ecotone in creosote bush habitat, is tightly clumped on function 1 but scattered on function 2. The ecotone defined by vegetation ended between the 9-m and 21-m trapping transects into both habitats.

Twelve lizard species were captured (677 individuals) in nine genera (Appendix A). In addition, there were 482 recaptures. The most abundant lizard was *A. tigris* (43.7% of total captures), with three times more individuals captured than the second most abundant species, *P. cornutum* (14.5% of total captures). A total of 128 *A. tigris* individuals were recaptured 314 times. Based on recapture data, eight of these individuals crossed the ecotone during the study. There were 42 recaptures of 26 individuals of *P. cornutum*, 7 individuals

Fig. 3. Discriminate function analysis of habitat variables grouped by distance from the ecotone. Function 1 is positively correlated with percent grass and percent bare soil and negatively correlated with percent creosote bush and percent yucca. Function 2 is positively correlated with percent grass and negatively correlated with percent bare soil and percent litter cover.

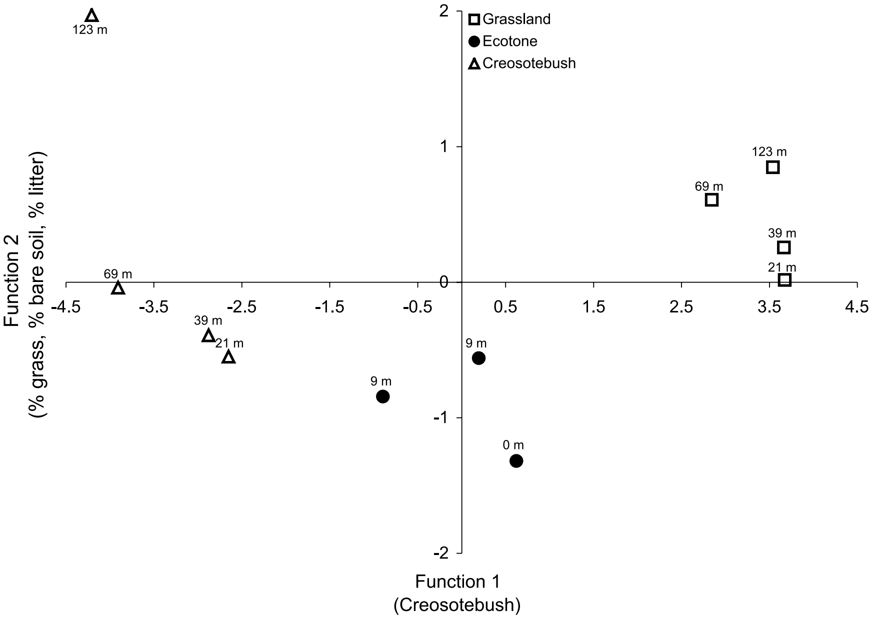


Table 1. Summary statistics of an 11-group discriminant function analysis and linear correlations (*r*) between original variables and discriminant functions.

Statistic	Discriminate function 1	Discriminate function 2
Eigenvalue	11.766	1.001
χ^2 test	134.434*	46.570 ns
df	60	45
% of variance	86.9	7.4
r		
Creosote bush (*Larrea tridentata*)	–0.955	–0.105
Litter	0.178	–0.536
Grass	0.310	0.753
Bare soil	–0.288	–0.625
Shrubs	0.107	–0.142
Yucca	0.048	0.331

Note: *, $p < 0.001$; ns (not significant), $p > 0.05$.

Table 2. Two-way ANOVA showing differences between mean numbers of captures per trap-day caused by habitat and species.

Assemblage parameter	df	Sums of squares	*F*	*p*
Habitat	2	0.0008	3.33	0.0422
Species	6	0.0282	41.52	<0.0001
Habitat × species	12	0.0036	2.65	0.0062

of which were recaptured after crossing the ecotone. Three species were caught only once during the two trapping seasons, *Cophosaurus texanus*, *Gambelia wislizenii*, and *Holbrookia maculata*. Only five individuals of *Crotaphytus collaris* were captured. *Aspidoscelis inornatus* was captured only in 2001 and only on one trapping transect located on the upper basin slope.

The two-way ANOVA revealed that habitat type, lizard species, and their interaction were significant predictors of capture success ($F_{[20,83]} = 15.13$, $p < 0.0001$, $r^2 = 0.83$) (Table 2). Lizard captures per trap-day increased with distance from the ecotone into both creosote bush and grassland habitat ($F_{[2,43]} = 13.06$, $p < 0.0001$, $r^2 = 0.389$) (Fig. 4). The increasing lizard abundance did not plateau by the trap array 123 m into either the grassland or creosote bush habitat. Significantly fewer lizards were captured in the ecotone than in the creosote bush and grassland habitats. Significantly fewer *A. tigris* were captured in the ecotone ($F_{[2,11]} = 7.27$, $p = 0.0132$), and more *A. uniparens* were captured in the grassland ($F_{[2,11]} = 15.68$, $p = 0.0012$) (Fig. 5).

Grassland habitat had the greatest species richness with 11 species, whereas the ecotone and creosote bush habitats both had 9 species. Species accumulated in the creosote bush habitat more quickly than in both the grassland and ecotone habitats. The species accumulation curve for the grassland habitat never reached an asymptote. At the end of the first trapping season, seven species had been captured in grassland, six in creosote bush, and five in the ecotone habitat. In the second trapping season, four additional species were captured in the grassland, three in the creosote bush, and four in the ecotone habitat. No new species were captured in any habitat after the 56th trapping day.

Discussion

The purpose of my study was to determine if diversity and abundance of a desert lizard community changed across a desert grassland – creosote bush ecotone. The analysis of vegetation suggested that the ecotone was approximately 26 m wide. This result is similar to that found by Wondzell et al. (1996) for the same ecotone based on their analysis using soil type. Each transect of 11 trap arrays grouped into three habitats: four trap arrays in the grassland (21–123 m), three middle trap arrays in the ecotone, and four trap arrays in the creosote bush (21–123 m). The grassland sites are

Fig. 4. Quadratic regression of total number of lizards captured with increasing distance from the ecotone. Lizard captures were standardized for differential trapping effort between years.

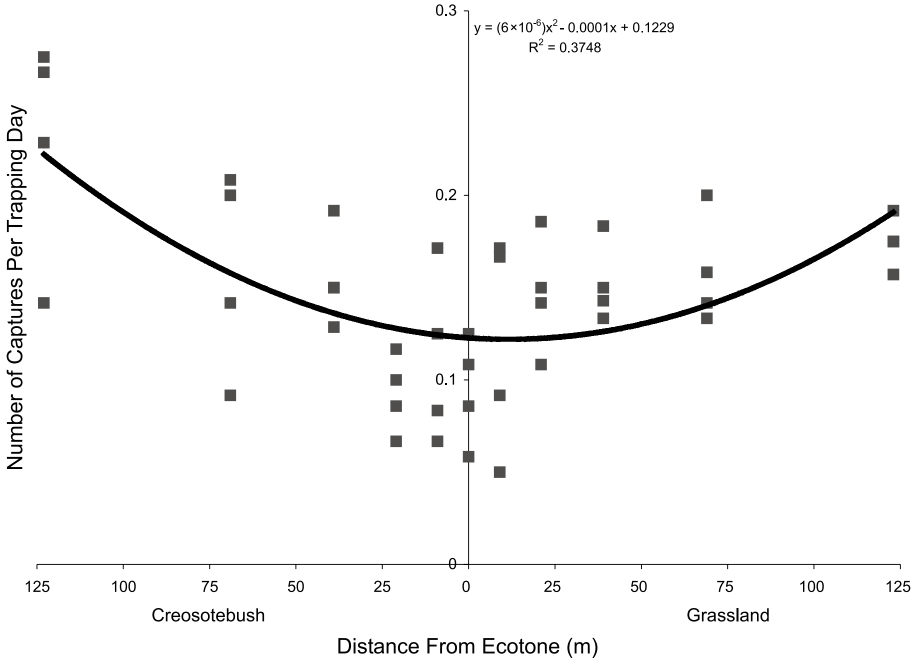
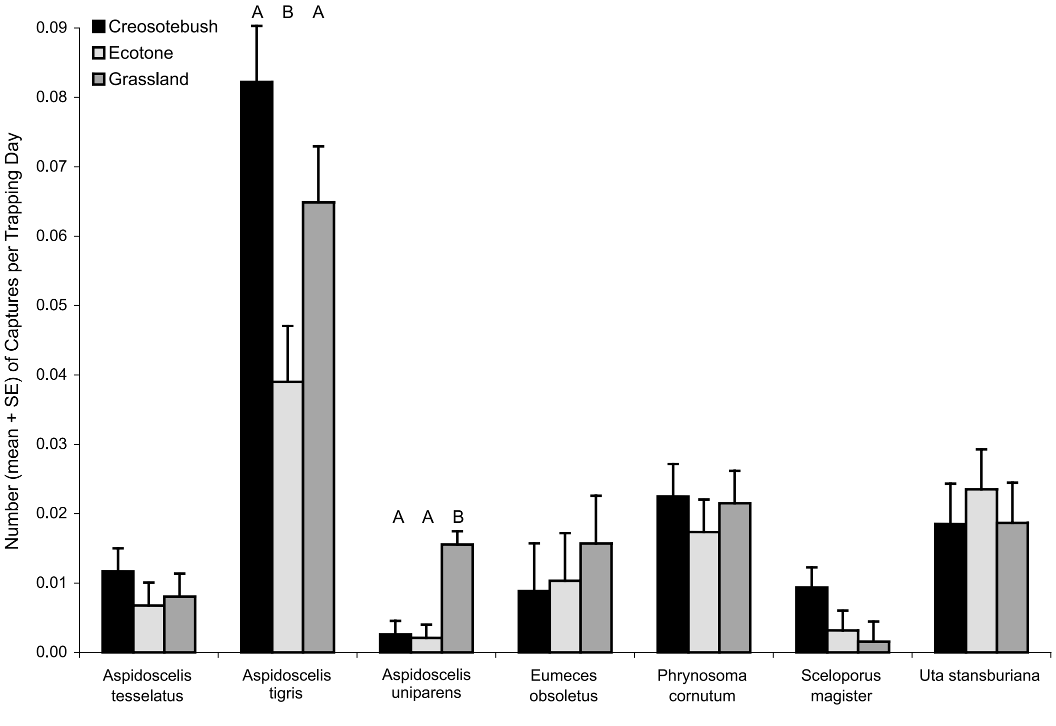


Fig. 5. Number of each lizard species captured in each habitat. Letters signify significant differences between habitats. All values are means ± 1 SE.



similar to each other in terms of vegetative profile, whereas creosote bush sites are more variable.

Total lizard abundance changed dramatically across the ecotone, significantly increasing with distance away from the ecotone irrespective of habitat (Fig. 4). This pattern of reduced total lizard abundance in the ecotone is the same pattern seen in each individual lizard species rather than being a consequence of the creosote bush and grassland habitats each possessing distinct specialist lizard communities (Fig. 5). Every common species could be found throughout the grassland and extending up to 70 m into the creosote bush habitat. *Holbrookia maculata* was observed only in grassland habitat. *Cophosaurus texanus* was seen near arroyos in all three habitats. *Aspidoscelis uniparens* was a grassland specialist, and *A. tigris* preferred either grassland or creosote bush to the ecotone habitat. *Eumeces obsoletus* did not have a significant habitat preference, but when it was captured in creosote bush habitat, it was always when a patch of grass or an arroyo was nearby. *Sceloporus magister* is typically a xeroriparian arboreal species, and when captured in grassland habitat, it was always associated with some form of shrub or yucca. *Uta stansburiana* demonstrated a unique trend among the lizards; it attained greatest abundance 123 m into both grassland and creosote bush habitats and exhibited a third peak in the ecotone. The peak in the ecotone is probably due to a large number of newly hatched neonates captured there on one transect on the lower piedmont slope. *Phrynosoma cornutum*, the other numerically dominant species, was ubiquitous in grassland and creosote bush habitats. Based on field observations, the large lizard predator *G. wislizenii*, of which only one neonate was captured in the creosote bush habitat, was common in all habitats but was observed to avoid pitfall traps. The other large lizard predator, *C. collaris*, was never observed in the creosote bush habitat.

Creosote bush and ecotone habitats had slightly reduced species richness compared to grassland habitat. Lizard species richness may have been elevated in the creosote bush habitat owing to the increased microhabitat diversity associated with nearby arroyos. The presence of arroyos may account for the greater variability in the creosote bush sites on DFA function 2 (Fig. 3) compared with the grassland sites.

Mechanisms

Desert lizards partition the environment on three main axes: time, space, and food (Pianka 1973). This leads to three potential explanations for the observed decrease in lizard abundance at the ecotone: decreased prey abundance, increased predation risk, and unique habitat requirements. Risk of predation can be closely linked to prey abundance, time of activity, and habitat. An area abundant in food resources may also have a greater risk of predation. Habitat requisites and diversity of microhabitats are also correlated with potential abundance and type of food resources.

Predator abundance and type of predator differ in different habitat types. Reports of increased bird nest predation and abundance of mammalian predators with proximity to an edge are common in the literature (Ricklefs 1989; Soderstrom et al. 1998). Common lizard predators at the Jornada are snakes (including species of the genera *Hypsiglena*, *Masticophis*, *Rhinocheilus*, and *Salvadora*), lizards of the genera *Crotaphytus* and *Gambelia*, and birds (including *Geococcyx californianus* and *Buteo swainsoni*) (Degenhardt et al. 1996; Holte and Houck 2000; Rodriguez-Estrella 2000). *Buteo swainsoni* has been observed patrolling the ecotone and anthropogenic fenceline edges on the Mount Summerford bajada (W.G. Whitford, personal communication).

Lizards can recognize habitat structure and organization. *Anolis* can identify structural differences in the surrounding environment and choose the habitat that they are familiar with when offered a binary choice between grass and shrub habitats (Kiester et al. 1975). As such, it is possible that the lizard species do not recognize the ecotone habitat studied here as having the correct requisites. There was considerable movement by lizards within a habitat but not between habitats. Of 482 recaptures, only 17 were recaptured having crossed the ecotone. This needs to be further tested using radiotelemetry. Root et al. (1999) found that a shrub–dune complex in the Chihuahuan Desert acted as a barrier to migration for small mammals.

Microhabitat diversity is often more important than macrohabitat type as a predictor for lizard communities (Pianka 1967; Schoener 1974; Szaro and Belfit 1986). Creosote bush habitat is depauperate in microhabitat diversity relative to both grassland and ecotone habitats. Lizards may have an advantage in detecting and escaping snake and terrestrial predators owing to the large areas of bare ground but may also be more susceptible to aerial predators. The ecotone habitat is spatially the smallest habitat, having a breadth of approximately 26 m. Shrubs tended to be smaller in the ecotone and did not have overlapping canopy coverage. Lizards in either the grassland or the creosote bush habitat have greater vegetative cover than those in the ecotone.

Conclusions

This study suggests that lizard abundance and community structure may be profoundly impacted by desertification of desert grasslands and the concomitant expansion of ecotonal habitat. On the Mount Summerford bajada, the creosote bush habitat forms a ring, isolating grassland sites on the upper piedmont slope from grassland sites on the upper basin slope and playa. The edge formed by the grassland – creosote bush ecotone may be acting as a barrier to dispersal, thereby isolating populations of grassland lizards from each other. Whitford and Creusere (1977), in a trapping study of lizards in the playa and lower basin slopes of Mount Summerford, demonstrated that immigration from other grassland habitats is an important component of the lizard community. Lizards on the piedmont slopes would emerge and reproduce earlier in the season. With the invasion of creosote bush into the Jornada basin, and desertification of desert grasslands in general (Buffington and Herbel 1965), the ability of lizards to move from one area to another may be seriously hampered.

Differences in lizard community structure across natural ecotones and anthropogenic edges in deserts are of increasing importance. Habitat is changing or being lost at a rapid rate because of desertification, ranching, development, and the increase in off-road vehicles (Buffington and Herbel 1965; Beauchamp et al. 1998). The transformation of grassland habitat to shrub-dominated habitat may result in a loss or restructuring of the lizard fauna. This can have a broad effect on organismal community structure because of the important position that lizards occupy in desert habitats (Pianka 1986).

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References

Barbault, R., and Maury, E. 1981. Ecological organization of a Chihuahuan Desert lizard community. Oecologia, **51**: 335–324.

Beauchamp, B., Wone, B., Bros, S., and Kutilek, M. 1998. Habitat use of the flat-tailed Horned Lizard (*Phrynosoma mcallii*) in a disturbed environment. J. Herpetol. **32**: 210–216.

Buffington, L.C., and Herbel, C.H. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. Ecol. Monogr. **35**: 139–164.

Colwell, R.K. 1997. EstimateS: statistical estimation of species richness and shared species from samples. University of Connecticut, Storrs, Conn. Available from http://viceroy.eeb.uconn.edu/estimates [accessed 10 March 2002].

Conroy, S. 1999. Lizard assemblage response to a forest ecotone in Northeastern Australia: a synecological approach. J. Herpetol. **33**: 409–419.

Degenhardt, W.G., Painter, C.W., and Price, A.H. 1996. Amphibians and reptiles of New Mexico. University of New Mexico Press, Albuquerque, N.M.

Fagan, W.F., Cantrell, R.S., and Cosner, C. 1999. How habitat edges change species interactions. Am. Nat. **153**: 165–182.

Fortin, M., Olson, R.J., Ferson, S., Iverson, L., Hunsaker, C., Edwards, G., Levine, D., Butera, K., and Klemas, V. 2000. Issues related to the detection of boundaries. Landsc. Ecol. **15**: 453–466.

Gibbens, R.P., and Beck, R.F. 1988. Changes in grass basal area and forb densities over a 64-year period on grassland types of the Jornada Experimental Range. J. Range Manag. **41**: 186–192.

Gosz, J.R. 1993. Ecotone hierarchies. Ecol. Appl. **3**: 369–376.

Harris, L.D. 1984. The fragmented forest: island biogeographic theory and the preservation of biotic diversity. University of Chicago Press, Chicago, Ill.

Harris, L.D. 1988. Edge effects and conservation of biotic diversity. Conserv. Biol. **2**: 330–332.

Holte, A.E., and Houck, M.A. 2000. Juvenile Greater roadrunner (Cuculidae) killed by choking on a Texas horned lizard (Phrynosomatidae). Southwest. Nat. **45**: 74–76.

Huenneke, L.F., Clason, D., and Muldavin, E. 2001. Spatial heterogeneity in Chihuahuan Desert vegetation: implication for sampling methods in semi-arid ecosystems. J. Arid Environ. **47**: 257–270.

Hurlbert, S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology, **52**: 577–586.

Johnston, C.A. 1993. Material fluxes across wetland ecotones in northern landscapes. Ecol. Appl. **3**: 424–440.

Kiester, A.R., Gorman, G.C., and Arroyo, D.C. 1975. Habitat selection behavior of three species of *Anolis* lizards. Ecology, **56**: 220–225.

Moreno, C.E., and Halffter, G. 2000. Assessing the completeness of bat biodiversity inventories using species accumulation curves. J. Appl. Ecol. **37**: 149–158.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. **10**: 58–62.

Pianka, E.R. 1967. On lizard species diversity: North American flatland deserts. Ecology, **48**: 333–351.

Pianka, E.R. 1973. The structure of lizard communities. Annu. Rev. Ecol. Syst. **4**: 53–74.

Pianka, E.R. 1986. Ecology and natural history of desert lizards. Princeton University Press, Princeton, N.J.

Ricklefs, R.E. 1989. Nest predation and the species diversity of birds. Trends Ecol. Evol. **4**: 184–186.

Risser, P.G. 1993. Ecotones at local to regional scales from around the world. Ecol. Appl. **3**: 367–368.

Rodriguez-Estrella, R. 2000. Breeding success, nest-site characteristics, and diet of Swainson's hawk (*Buteo swainsoni*) in a stable population in northern Mexico. Can. J. Zool. **78**: 1052–1059.

Root, J.J., Jorgensen, E.E., and Demarais, S. 1999. Effects of a habitat boundary on small mammals associated with the white sands dune complex. Southwest. Nat. **44**: 193–198.

Sartorius, S.S., Vitt, L.J., and Colli, G.R. 1999. Use of naturally and anthropogenically disturbed habitats in Amazonian rainforest by the teiid lizard *Ameiva ameiva*. Biol. Conserv. **90**: 91–101.

SAS Institute Inc. 2001. JMP [computer program]. Version 4.0.4. Duxbury Press, Pacific Grove, Calif.

Schlaepfer, M.A., and Gavin, T.A. 2001. Edge effects on lizards and frogs in tropical forest fragments. Conserv. Biol. **15**: 1079–1090.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science (Wash., D.C.), **185**: 27–39.

Soderstrom, B., Part, T., and Ryden, J. 1998. Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. Oecologia, **117**: 108–118.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry. W.H. Freeman and Co., New York, N.Y.

SPSS Inc. 1999. SPSS [computer program]. Version 10.0. SPSS Inc., Chicago, Ill.

Szaro, R.C., and Belfit, S.C. 1986. Hertpetofaunal use of a desert riparian island and its adjacent scrub habitat. J. Wildl. Manag. **50**: 752–761.

Whitford, W.G., and Creusere, F.M. 1977. Seasonal and yearly fluctuations in Chihuahuan Desert lizard communities. Herpetologica, **33**: 54–65.

Wierenga, P.J., Hendrickx, J.M.H., Nash, M.H., Ludwig, J., and Daugherty, L.A. 1987. Variation of soil and vegetation with distance along a transect in the Chihuahuan Desert. J. Arid Environ. **13**: 53–63.

Wondzell, S.M., Cunningham, G.L., and Bachelet, D. 1996. Relationships between landforms, geomorphic processes, and plant communities on a watershed in the northern Chihuahuan Desert. Landscape Ecol. **11**: 351–362.

Appendix A

Table A1. Number of lizard captures at each distance from the edge for every transect in 2000 and 2001.

	Aspidoscelis tesselatus	*Aspidoscelis inornatus*	*Aspidoscelis tigris*	*Aspidoscelis uniparens*	*Cophosaurus texanus*	*Crotaphytus collaris*	*Eumeces obsoletus*	*Gambelia wislizenii*	*Holbrookia maculata*	*Phrynosoma cornutum*	*Sceloporus magister*	*Uta stansburiana*
2000												
Trap A												
123G	1	0	3	3	0	1	6	0	0	0	0	1
69G	0	0	5	1	0	0	4	0	0	0	0	0
39G	1	0	7	2	0	0	2	0	0	0	0	0
21G	3	0	2	0	0	0	2	0	0	1	0	0
9E	1	0	0	0	0	0	1	0	0	0	0	0
0E	0	0	5	0	0	0	1	0	0	1	0	0
9E	2	0	3	0	0	0	1	0	0	2	1	0
21C	0	0	1	1	0	0	0	0	0	2	0	0
39C	2	0	5	0	0	0	0	1	0	1	1	1
69C	1	0	4	0	0	0	4	0	0	1	0	1
123C	1	0	3	0	0	0	2	0	0	2	0	1
Trap B												
123G	0	0	6	2	0	0	0	0	0	1	0	4
69G	0	0	5	3	0	0	0	0	0	1	0	3
39G	0	0	6	0	0	0	0	0	1	2	0	2
21G	0	0	5	1	0	0	0	0	0	3	0	2
9E	2	0	4	0	0	0	1	0	0	1	0	3
0E	0	0	0	0	0	1	0	0	0	1	0	1
9E	0	0	1	0	0	0	0	0	0	0	0	0
21C	2	0	3	1	0	0	0	0	0	2	0	2
39C	2	0	3	0	0	0	1	0	0	1	3	0
69C	0	0	6	0	0	0	0	0	0	7	2	2
123C	2	0	10	0	0	0	0	0	0	2	0	2
Trap C												
123G	0	0	5	1	0	0	0	0	0	4	0	0
69G	1	0	3	0	0	0	0	0	0	2	1	0
39G	0	0	5	0	0	0	0	0	0	0	0	3
21G	0	0	3	0	0	0	1	0	0	0	1	2
9E	0	0	2	0	0	0	0	0	0	0	0	3
0E	1	0	4	0	0	0	0	0	0	1	2	2
9E	1	0	3	0	0	0	0	0	0	0	0	1
21C	0	0	2	0	0	0	1	0	0	1	0	1
39C	0	0	5	0	0	0	0	0	0	5	1	0
69C	0	0	4	0	0	0	0	0	0	0	1	0
123C	1	0	8	0	0	0	2	0	0	2	2	1

Table A1 (*continued*).

	Aspidoscelis tesselatus	*Aspidoscelis inornatus*	*Aspidoscelis tigris*	*Aspidoscelis uniparens*	*Cophosaurus texanus*	*Crotaphytus collaris*	*Eumeces obsoletus*	*Gambelia wislizenii*	*Holbrookia maculata*	*Phrynosoma cornutum*	*Sceloporus magister*	*Uta stansburiana*
2001												
Trap A												
123G	1	0	0	0	0	1	2	0	0	1	0	1
69G	0	0	2	0	0	0	3	0	0	1	0	0
39G	1	0	2	0	0	0	1	0	0	2	0	0
21G	2	0	2	1	0	1	2	0	0	1	0	1
9E	1	0	1	0	0	0	1	0	0	0	0	1
0E	0	0	1	0	0	0	3	0	0	0	0	2
9E	0	0	4	0	0	0	0	0	0	1	1	0
21C	0	0	4	1	0	0	1	0	0	2	0	0
39C	1	0	3	0	0	0	0	0	0	1	1	1
69C	1	0	2	0	0	0	0	0	0	1	0	2
123C	0	0	5	0	0	0	0	0	0	2	0	1
Trap B												
123G	0	0	4	1	0	0	0	0	0	1	0	4
69G	2	0	3	0	0	0	0	0	0	0	0	2
39G	0	0	5	2	0	1	2	0	0	1	0	0
21G	0	0	2	2	0	0	0	0	0	1	0	1
9E	0	0	3	0	0	0	0	0	0	2	1	3
0E	0	0	0	1	0	0	0	0	0	0	0	3
9E	0	0	2	1	0	0	0	0	0	0	0	4
21C	0	0	1	0	0	0	1	0	0	0	2	0
39C	2	0	5	1	0	0	0	0	0	0	2	3
69C	1	0	4	1	0	0	0	0	0	1	0	1
123C	2	0	6	0	0	0	2	0	0	3	0	4
Trap C												
123G	0	0	5	1	0	0	0	0	0	3	1	1
69G	0	0	6	1	1	0	0	0	0	2	0	0
39G	0	0	6	1	0	0	0	0	0	1	0	0
21G	0	0	0	1	0	0	0	0	0	3	0	2
9E	0	0	1	0	0	0	0	0	0	3	0	2
0E	0	0	2	0	0	0	0	0	0	1	1	1
9E	0	0	3	1	0	0	0	0	0	0	0	1
21C	0	0	0	0	0	0	1	0	0	0	0	2
39C	1	0	3	0	0	0	1	0	0	0	2	0
69C	0	0	4	0	0	0	0	0	0	0	0	2
123C	0	0	12	0	0	0	1	0	0	2	1	0
Trap D												
123G	1	4	4	0	0	0	0	0	0	1	0	1
69G	0	1	8	0	0	0	2	0	0	0	0	2

Table A1 (*concluded*).

	Aspidoscelis tesselatus	*Aspidoscelis inornatus*	*Aspidoscelis tigris*	*Aspidoscelis uniparens*	*Cophosaurus texanus*	*Crotaphytus collaris*	*Eumeces obsoletus*	*Gambelia wislizenii*	*Holbrookia maculata*	*Phrynosoma cornutum*	*Sceloporus magister*	*Uta stansburiana*
39G	1	1	4	0	0	0	1	0	0	2	0	0
21G	0	3	2	0	0	0	0	0	0	3	0	1
9E	1	3	5	1	0	0	3	0	0	1	0	1
0E	0	0	2	0	0	0	1	0	0	1	0	2
9E	0	1	5	2	0	0	0	0	0	5	0	1
21C	0	1	3	0	0	0	0	0	0	1	0	1
39C	0	2	7	0	0	0	0	0	0	0	0	0
69C	0	0	12	1	0	0	0	0	0	2	0	0
123C	2	0	10	0	0	0	0	0	0	0	0	4

Note: G, grassland habitat; E, ecotone habitat; C, creosote bush (*Larrea tridentata*) habitat.