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## **Boundary processes between a desert sand dune community and an encroaching suburban landscape**

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### **Abstract**

In contrast to the body of work in more mesic habitats, few studies have examined boundary processes between natural and anthropogenic desert landscapes. Our research examined processes occurring at boundaries between a desert sand dune community and an encroaching suburban habitat. We measured responses to an anthropogenic boundary by species from multiple trophic levels, and incorporated measures of habitat suitability, temporal variation, and spatial scales. At an edge versus core habitat scale the only aeolian sand species that demonstrated an unambiguous negative response to the anthropogenic habitat edges was the flat-tailed horned lizard (*Phrynosoma mcallii*). Conversely loggerhead shrikes (*Lanius ludovicianus*) demonstrated a positive response to that edge. At a finer scale, species that exhibited a response to a habitat edge within the first 250 m included the horned lizards along with desert kangaroo rats (*Dipodomys deserti*). The latter species' response was confined to 25 m from the edge. For the flat-tailed horned lizard, edge effects were measured up to 150 m from the habitat boundary. Three potential causal hypotheses were explored for explaining the edge effect on horned lizards: 1) potential invasions of exotic ant species

Barrows, C. W., et al.

reducing potential prey for the lizards; 2) road avoidance and road associated mortalities; and, 3) predation from a suite of avian predators whose occurrence and abundance may be augmented by resources available in the suburban habitat. We rejected exotic ant hypothesis due to the absence of exotic ants within the boundary region, and because native ant species (prey for horned lizards) did not show an edge effect. Our data supported the predation hypothesis and road mortality hypotheses. Mechanisms for regulating population dynamics of desert species are often “bottom-up,” stochastic processes driven by precipitation. The juxtaposition of an anthropogenic edge appears to have created a shift to a “top-down,” predator mediated dynamic for these lizards.

*Keywords:* Edge Effect; Anthropogenic boundary processes; Desert aeolian sand community; Flat-tailed horned lizard; Loggerhead shrike; Predation

## **1. Introduction**

Primary mechanisms that distinguish processes at habitat boundaries include: 1) abiotic gradients unique to those boundaries, 2) access to spatially separated resources, and 3) species interactions (Wiens et al. 1985, Murcia 1995, Laurance et al. 2002, Ries et al. 2004). Collectively these mechanisms create a conceptual framework for understanding ecological boundary responses. Additionally, understanding factors that control the occurrence and dynamics of populations in relatively unfragmented habitat patches provide a context from which to evaluate how those drivers are impacted at boundaries. In arid ecosystems highly variable and unpredictable precipitation often regulates biological processes (Noy-Meir, 1973). Support for this axiom can be found

Barrows, C. W., et al.

across a broad range of taxa and regions (Mayhew 1965, 1966; Pianka 1970; Ballinger 1977; Whitford and Creusere 1977; Seely and Louw 1980; Dunham 1981; Abts 1987; Robinson 1990; Brown and Ernest 2002; Germano and Williams 2005). Population dynamics of desert species are thus often characterized as being regulated from the bottom-up, by resource availability mediated by annual rainfall (Brown and Ernest 2002). In contrast, Faeth et al. (2005) described a shift in the processes controlling population dynamics in a suburban desert environment. There irrigated landscapes regulated productivity and resulted in a predation controlled, top-down community. These different population regulating processes meet at the boundary between natural desert and anthropogenic habitats. The extent to which processes generated by anthropogenic habitats encroach on the natural desert and impact components of that community is the subject of this paper.

In contrast to the body of work in more mesic habitats, few studies have examined boundary processes between natural and anthropogenic desert landscapes (e.g., Germaine et al. 1998, Germaine and Wakeling 2001, Boal et al. 2003, Gutzwiller and Barrow 2003). Here we examined processes and species occurring at boundaries between an aeolian sand landscape and encroaching suburban and abandoned agricultural field habitats. Distinguishing between variance in abundance imposed by the heterogeneity of the available habitats and what if any effects the proximity of an edge has on the distribution of native species is critical in determining the ecological importance of those edges (Bolger et al. 1997, Fagan et al. 2003). We incorporated measures of habitat suitability, temporal variation, and spatial scales to identify whether components of an aeolian sand community have altered their distributions in response to the presence of

Barrows, C. W., et al.

anthropogenic habitat edges.

Much of the previous research on edges has focused on temperate and tropical habitats (Janzen 1983, Wilcove 1985, Laurance 1991, Murcia 1995, Laurance et al. 2002, Watson et al. 2004) where boundary-mediated ecological flow processes extend from 10-400 m into interior habitats (i.e., Kapos 1989, Camargo and Kapos 1995, Laurance et al. 2001). Fewer studies have investigated edge effects in semi-arid environments, with much of that work focusing on coastal sage scrub in southern California (Bolger et al. 1991, Bolger et al. 1997, Kristan et al. 2003). In this habitat, moisture gradients at suburban-natural community boundaries have limited the invasion of non-native ants to 100 m or more into the natural communities from mesic refuges in the suburban landscape, with a corresponding negative cascade affecting overall native species richness (Suarez et al. 1998). Increased predation is another factor identified at sage scrub boundaries (Bolger et al. 1991, Bolger et al. 1997, Crooks and Soulé 1999, Suarez et al. 2000, Suarez and Case 2002, Unfried 2003). Collectively these findings define the range of anthropogenic boundary impacts described to date. Our objective was to determine whether any of these impacts also influence the distribution and abundance of species in desert habitats.

## **2. Methods**

### *2.1 Study Area*

Aeolian sand habitats were studied within the Thousand Palms Preserve (33° 47' N, 116° 20' W) in the Coachella Valley near Palm Desert, Riverside County, California. The Preserve includes approximately 1,300 ha of contiguous sand dunes and hummocks.

Barrows, C. W., et al.

The Coachella Valley is an extremely arid shrub desert with a mean annual rainfall of 79 to 125 mm (most recent 60 year means, Western Regional Climate Center, Palm Springs and Indio reporting stations). The lowest rainfall year occurred in 2002, with just 4 to 7 mm recorded across the valley floor. Temperatures range from a low approaching 0 °C in the winter to highs exceeding 45 °C commonly recorded during July and August.

Study plots were designed to enable analyses at both a coarse scale (edge versus interior plots) and at a finer scale along the habitat edges (within plot distance from the habitat edge). Additionally, study plots were established to identify effects from two separate edge types. Fourteen study plots were established within the Preserve: three were located along a 2.4 km boundary with a suburban golf course community, six were located along a 3.2 km boundary with an abandoned agricultural area and sparse rural housing (Figure 1), and five control plots were centrally located in “core” habitat, greater than 500 m from roads. There was a four-lane paved road separating the Preserve from the suburban habitat and a two-lane paved road separating the Preserve from an area of abandoned agriculture. All study plots were located in a stratified random manner. Plots were stratified so as to include both active sand dune and sand hummock habitat in a proportion corresponding to the aerial extent of those different habitat types. Edge plots were established adjacent to paved roads, but randomly located along the roadway.

Each of the 14 study plots consisted a cluster of 5-8, 10 m x 100 m belt transects. Edge plots included seven transects, with the first centered on a barbed wire boundary fence and running parallel to the fence and adjacent paved road. A second transect was established parallel to the first, but was 25 m interior from the edge. Additional parallel transects were placed at 50, 100, 150, 200, and 250 m from the edge. Core plots consisted

Barrows, C. W., et al.

of similar clusters of belt transects with the same dimensions as the edge sites. Core plots were >500 m from any roadway, residence, or habitat discontinuity and included five to eight parallel belt transects separated by 50-150 m. Each transect was marked with a short wooden stake at the beginning, middle, and end so that their position with respect to the boundaries of the belt transect could be readily determined. Each study plot covered approximately 2.5 ha. Surveys were repeated six times at each plot between June and July each year from 2002 through 2004. Data collected in 2002 focused on flat-tailed horned lizards, *Phrynosoma mcallii*. Data collected in 2003 and 2004 included all species encountered.

## *2.2 Survey Protocol*

The fine aeolian sand of the Thousand Palms Preserve presented an opportunity unique to sand dunes to quantify the occurrence and abundance of all terrestrial species occurring along transects with more or less equal detectability. Each vertebrate species could be identified to species and age class by their diagnostic tracks left in the sand. Ground-based species left easily identifiable tracks, and so their ability to avoid detection by differences in activity times, cryptic coloration, or stealthy behavior was nullified. Because late afternoon and evening breezes would wipe the sand clean the next day's accumulation of tracks could not be confused with those from the previous day. On those days when the wind did not blow, tracks from the current day could be distinguished from those from previous days by whether or not the tracks of nocturnal arthropods crossed over the vertebrate's track. Lizard track identification criteria were developed by

Barrows, C. W., et al.

spending several weeks prior to surveys, following tracks until animals were located and the species and age class was confirmed. Tracks from other diurnal vertebrates were confirmed as they were encountered during pre-survey field work. Nocturnal or otherwise cryptic species' tracks were confirmed by comparisons with foot sizes and configurations from museum specimens

Surveys would begin after the sand surface temperature had risen sufficiently so that diurnal reptiles were observed to be active, usually  $\geq 35^{\circ}$  C. Surveys continued until late morning when the high angle of the sun reduced the observer's ability to distinguish and identify tracks. One or two observers working in tandem completed a survey on a given study plot in 30-45 minutes, recording all fresh tracks observed within the 10 m wide belt of each 100 m transect. Tracks were followed off transect if it was necessary to confirm a species' identification and to insure that the same individual was not crossing the same transect repeatedly, thus avoiding an inflated count of the individuals active on that transect. Data for separate transects were considered independent for most species. In addition to tracks, we recorded any sightings of animals along transects and recorded any bird vocalizations heard during a survey. Wide ranging predators such as coyotes (*Canis latrans*), greater roadrunners (*Geococcyx californianus*), American kestrels (*Falco sparverius*), and loggerhead shrikes (*Lanius ludovicianus*), had ranges much larger than the transect dimensions, and so were recorded as present on a study plot, rather than on individual transects.

Harvester Ants (*Pogonomyrmex* sp.) were sampled using dry pitfall traps in April of each year. Previous arthropod sampling efforts (Barrows, unpublished data) have indicated that in most years ant numbers reached peak numbers in April. This was also

Barrows, C. W., et al.

the period when lizards eating ants would be consuming the resources necessary for egg production in the coming months. Three pitfall traps was placed on each transect; one at both ends and another at the transect middle. The traps were collected within 24 hrs of being set out to avoid any mortality of vertebrates that happened into the traps. Ant data were presented as the total count per transect.

### *2.3 Habitat Measures*

Vegetation density and plant species composition were measured on each transect each year. All perennial shrubs were counted within the 10 m x 100 m belt transects. Annual plants were counted and cover estimated in a 1 m<sup>2</sup> sampling frame placed at 12 locations along the midline of the belt transect.

Sand compaction has been described as a key habitat variable for Coachella Valley fringe-toed lizards, *Uma inornata*, (Barrows 1997), and may be important for other psammophilic species. Sand compaction was measured at 25 points, approximately four m apart, along the midline of each belt transect using a hand-held penetrometer with an adapter foot for loose soils (Ben Meadows Company, Janesville, WI, USA).

### *2.4 Data Analysis*

A one-way analysis of variance (ANOVA) was employed to conduct coarser scale analyses, examining edge versus core differences, and to include wider ranging bird species. Here edge plots adjacent to the preserve edge (including transects ranging from 0

– 250 m from that edge) were compared with core plots (> 500 m from the preserve edge). A two-way ANOVA was conducted to partition finer scale variance in species abundance between the treatment (distance from the preserve edge) and variance associated with habitat heterogeneity between each of the edge plots.

For the nine edge plots, those species that showed statistically significant variation with respect to distance to edge (0-250 m) were then subjected to a linear regression to determine whether environmental variation coincident with the edge distance could explain that observed variance. All variables were tested for normality and transformed with natural logs when necessary. Dependent variables were means of the six surveys on each transect per year for each species. Independent variables included measures of sand compaction ( $\text{kg} / \text{cm}^2$ ) for each year, shrub density ( $\text{shrubs} / \text{m}^2$ ), and linear distance from the Preserve edge. Total observations equaled 63 (seven transects / plot over nine plots), and just since one or two variables were included in the regression analyses, model over fitting was avoided. Linear regression analyses were performed using SYSTAT 10.0 (SYSTAT, Wilkinson, 1990). A threshold of  $\alpha = 0.05$  for statistical significance was used throughout this paper.

### **3. Results**

Of the nine species tested with ANOVAs at the edge versus core scale, only the flat-tailed horned lizard and the loggerhead shrike showed a statistically significant effect, although their responses were opposite (Table 1). Shrikes were more common along the edge whereas the horned lizards were more abundant in the core. At the finer scale, for those nine plots situated along the Preserve boundary, distance from the

Barrows, C. W., et al.

Preserve edge was found to be a significant source of variance for the flat-tailed horned lizard, and the Desert kangaroo rat, *Dipodomys deserti* (Table 2).

These statistical results are corroborated by the patterns of temporal and spatial species' abundance for the seven sand dune occurring species included in our analysis (Figs. 2a-2g). There were no consistent responses to proximity of the habitat boundary for Coachella Valley round-tailed ground squirrels (*Spermophilus tereticaudus chlorus*), sidewinders (*Crotalus cerastes*), western shovel-nosed snakes (*Chionactis occipitalis*), and harvester ants (*Pogonomyrmex* spp., including *P. californicus* and *P. magnacanthus*). The abundance of both fringe-toed lizards and desert kangaroo rats appeared to be reduced along the immediate habitat edge in both 2003 and 2004, but not at distances  $\geq$  25 m from that boundary in either year. In contrast, flat-tailed horned lizards' abundance was reduced at distances from the habitat edge of 150 m in 2002, and 100 m in 2003 and 2004.

For the nine edge plots, Pearson's correlations were calculated for distance from the habitat edge and sand compaction and shrub density. Edge distance was not correlated with sand compaction ( $r = -0.001$  to  $-0.135$ , all  $P = .0335$  to  $0.995$ ), and was only moderately negatively correlated with shrub density ( $r = -0.235$ ,  $P = 0.043$ ). However, sand was consistently more compacted along the immediate Preserve boundary than it was 25 m interior of that boundary (paired t-test,  $p = 0.048$ ).

Regression models were run for the two species for which the within-plot ANOVAs indicated significant edge correlations (Table 3). Shrub density did not explain a significant amount of the variance in abundance for either species, and so was not included in the models. For each species, a single variate model using distance as the

Barrows, C. W., et al.

independent variable yielded statistically significant linear relationships. However, only the horned lizard's edge distance model yielded a  $R^2$  above 0.100. A single variate model using sand compaction as the independent variable also yielded a significant relationship for the horned lizard.

Boundaries between the natural desert and anthropogenic landscapes evaluated here were of two types. One was adjacent to a suburban golf course community, but separated by a well used four-lane road with curbs. The other boundary was adjacent to abandoned agricultural fields with tree rows surrounding each parcel, and was separated by a low use, two-lane road without curbs. The abundance of flat-tailed horned lizards, round-tailed ground squirrels, desert kangaroo rats and harvester ants differed between habitats adjacent to the two boundary types (Table 2). For species other than horned lizards, abundances within boundary types were statistically invariant on transects within plots; no difference in their response to the edge was detected. For the horned lizards there were differences in abundance with respect to the Preserve edge. No horned lizards were located closer than 100 m from the boundary adjacent to the suburban landscape; here lizard abundance didn't reach an apparent asymptote until 200 m from the preserve edge (Fig. 3). Some horned lizards were located right to the edge of the boundary along the abandoned agricultural fields. Abundance appeared asymptotic 100 m from the preserve edge

#### **4. Discussion**

We identified negative responses to anthropogenic boundaries for flat-tailed horned lizards, and desert kangaroo rats. Data for the horned lizards were the most

consistent from the standpoint of different scales (edge versus core plots and within-plot edge distances) and linear regression results. For the kangaroo rat, edge effects were apparent only at the finer scale, within-plot analyses and relatively weak regression results. This pattern may be explained by environmental variation associated with Preserve habitat boundary. Historic road grading created low berms along the road-Preserve boundaries. Rare flood events create pooled standing water and silt deposition along those berms, resulting in significantly more compacted sediments within 10-20 m of that boundary. The edge effect for desert kangaroo rats appeared to be confined to < 25 m from the Preserve boundary, coincident with the effects of roadside berms.

Flat-tailed horned lizards typically occupy sand compaction conditions found throughout the nine edge plots., Edge effects for this species were measured up to 150 m from the habitat boundary, well beyond the impact of the roadside berms. This lizard's range has been reduced and fragmented in recent years (Turner and Medica 1982) and this preserve may represent the only remaining habitat for flat-tails in the northern one-third of their original distribution. Deciphering causal factors for the flat-tail's absence along the preserve boundary may provide important directions for future management and preserve design strategies. Three non-exclusive hypotheses were evaluated to explain this edge effect.

1) Road Mortality – Road Avoidance Hypothesis - Like many reptiles, flat-tailed horned lizards will use the margins of paved roads, most likely for thermoregulation (Norris 1949, Turner and Medica 1982). Impacts of roads on wildlife populations include direct mortality and road avoidance (Forman and Alexander 1998). If there is a road impact here we would expect the response from the lizards to be stronger adjacent to

Barrows, C. W., et al.

larger, busier roadways. In fact, we found consistent differences in lizard-edge relationships between edges adjacent to a busy four-lane road and a less used two-lane road. While edge effects were apparent along each road type, lizards adjacent to the four-lane road demonstrated a more pronounced and abrupt edge effect than those along the two-lane road, and so the data are consistent with a road effect hypothesis. No statistical difference in shrike abundance was found between plots along the two-lane and four-lane roads, eliminating shrike predation as a confounding variable. The lack of an edge effect in any of the three nocturnal species included in our analysis may be in part a reflection of reduced vehicle traffic during the night.

2) Invasive Alien Ant Hypothesis - Flat-tailed horned lizards' prey is almost exclusively harvester ants (Pianka and Parker 1975, Turner and Medina 1982). The reduction in harvester ants from 2003 to 2004 in the aeolian sand habitat, which coincided with a similar reduction in flat-tails, supports a hypothesis that the population dynamics of these two taxa are linked.

Suarez and Case (2002) and Fisher et al. (2002) have identified the invasion of non-native Argentine ants (*Linepithema humile*) as a leading factor in the disappearance of coast horned lizards (*P. coronatum*) from fragmented habitats in coastal southern California. Suarez et al. (1998) described Argentine ants being able to invade up to 100 m into semi-arid natural habitats, greatly reducing native ant populations within that same 100 m belt. Coast horned lizards that were limited to Argentine ants for prey had negative or zero growth rates, and so could not maintain populations unless native ant populations were present (Suarez et al. 2000, Suarez and Case 2002).

Argentine ants were known to occur in adjacent suburban golf course

Barrows, C. W., et al.

communities. Similarly, introduced fire ants (*Solenopsis invicta*) have also been identified in the Coachella Valley and elsewhere are associated with roads, suburban development and edges (Forys et al. 2002), No non-native ant species were collected within any plots on the Thousand Palms Preserve.. The extreme aridity of this habitat may be a barrier to invasion of ant species otherwise problematic to more mesic habitats. These data, and the lack of any edge effect apparent in the native harvester ants, indicate that alien ant invasions are not a cause for the observed edge effect in the horned lizard population

3) Enhanced Predation Hypothesis - Increased predation along habitat edges is often identified as a causal factor for reducing nesting success for birds along forest edges (Andr n et al. 1985, Wilcove 1985, Angelstam 1986, Andr n and Angelstam 1988, Burkey 1993, Estrada et al. 2002, Maina and Jackson 2003, Aquilani and Brewer 2004). If increased levels of predation along the habitat margins are responsible for reduced flat-tail numbers there, then increased numbers of predators should be evident.

Comparing edge versus core plots, counts of loggerhead shrikes were consistently higher on edge of the aeolian sand habitat. The higher numbers of shrikes at edge plots versus core locations in our study area was consistent with an enhanced predator hypothesis. However, if predation rates are an important causal factor, then why were other species not similarly impacted? Of the six vertebrate species measured, three are primarily nocturnal and so would not be subjected to predation pressure from the diurnal shrikes; however Daley et al. (2000) did record shrike predation on four kangaroo rats. Of the diurnal potential prey species, the ground squirrel's large size puts them outside of the prey range of shrikes. The two lizards are within the shrikes' prey size, and flat-tailed

Barrows, C. W., et al.

horned lizards are regularly preyed on by shrikes (Young et al. 2004). Whereas both lizards are cryptically colored, flat-tailed horned lizards are slower moving and often respond to threats by remaining motionless (Norris 1949). Fringe-toed lizards respond to threats by running extremely fast or diving into the loose sand (Stebbins 1944).

Although predators were not quantified in 2002, flat-tailed horned lizards were commonly observed being preyed upon by American kestrels during site visits that year. Carcasses of marked horned lizards that had disappeared from study plots were located 0.7 km away in a palm tree planted on the edge of a golf course and frequented by kestrels. In 2003 and 2004 when predator occurrence was quantified, there were few observations of kestrels, but shrike observations were common. While kestrels and shrikes are native to the deserts of southern California, their abundance in the sand dune habitats of the Coachella Valley is likely enhanced by suburban development. In a pre-development landscape there were no trees growing in or around the Coachella Valley sand dunes. American kestrels are obligate hole or ledge nesters. Whereas there were once no nest sites for kestrels within 10 km of the dunes, today palm trees and other exotic vegetation planted in the neighboring suburban developments provide abundant nest sites on ledges formed by the large leaf petioles and in the thick “skirts” of dead palm leaves. While shrikes nest in native desert shrubs, trees in suburban areas as well as tree windbreaks planted at the margins agricultural fields provide more sheltered nest sites. Power poles bordering the preserve provide elevated perch sites for both the kestrels and shrikes to see prey and then launch their hunting sorties. Flat-tailed horned lizards may be subjected to levels of predation along edges that they would not likely have experienced in a pre-development landscape.

By collecting data on multiple species from multiple trophic levels we have rejected the alien ant hypothesis and found support for both the predation and road affect hypotheses. Dynamics of the flat-tailed horned lizard population occupying a 100-200 m boundary region of the available habitat appears to have shifted from a bottom-up process where the lizard numbers are regulated by native ant abundance, to a top-down process where the lizards are limited by predation, and possibly road mortality. This shift in regulatory processes may contribute to a habitat “sink” (Pulliam 1988) along the preserve boundary. For 2003 and 2004 combined, the horned lizards’ mean reproductive success ranged from 0 – 0.2 hatchlings/adult at distances from 0 to 150 m from the habitat edge; at 200 m from the edge and in core plots, mean reproductive success averaged 0.8 hatchlings/adult (Barrows, unpubl. data). Without immigration from the preserve core, flat-tailed horned lizards may not be able to sustain populations in the boundary region.

These results demonstrate the utility of community based research designed to evaluate hypotheses regarding processes that regulate the abundance of species (Barrows et al. 2005). Rather than having broad impacts from indeterminate causes, boundary effects here were found to have a narrow scope and likely causes were identified. These findings can allow managers to focus adaptive management strategies aimed at reducing the boundary effect for flat-tailed horned lizards and so improve the viability of this remnant population. In the face of increasing suburban expansion into natural desert communities in the southwestern U. S. and elsewhere in arid regions of the world, managers otherwise face decisions with little or no baseline from which to predict species responses.

Barrows, C. W., et al.

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Barrows, C. W., et al.

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Table 1. Analysis of variance (ANOVA) of the abundance of nine species at the larger, edge versus core, scale. The error term represents variation among plots. P-values  $\leq$  0.05 indicate a statistically significant amount of the variance in the distribution of that species is explained by that treatment (edge effect).

Species	Source of variation	SS	df	MS	F	P-value
Coachella Valley fringe-toed lizard	Edge effect	1.404	1	1.404	0.871	0.361
	Error	33.850	21	1.612		
Flat-tailed horned lizard	Edge effect	1.294	1	1.294	8.464	0.007
	Error	3.975	26	0.153		
Sidewinder	Edge effect	0.008	1	0.008	0.564	0.465
	Error	0.208	14	0.015		
Shovel-nosed snake	Edge effect	0.032	1	0.032	0.211	0.650
	Error	3.344	22	0.152		
Round-tailed ground squirrel	Edge effect	0.302	1	0.302	3.941	0.063
	Error	1.379	18	0.077		
Desert kangaroo rat	Edge effect	0.078	1	0.078	0.125	0.727
	Error	11.781	19	0.620		
Harvester ants	Edge effect	13.209	1	13.209	0.551	0.467
	Error	455.486	19	23.973		
Greater roadrunner	Edge effect	0.009	1	0.009	0.096	0.760
	Error	2.169	22	0.099		
Loggerhead shrike	Edge effect	1.131	1	1.131	18.871	0.0002
	Error	1.558	26	0.060		

Table 2. Two-way ANOVAs were employed to determine sources of variance at a smaller, within edge plot, scale. Here variance is partitioned between edge effects and between plots occurring along two boundary types. Coachella Valley fringe-toed lizards did not occur along the boundary that included the four-lane road, so only a one-way ANOVA was calculated for edge effect. P-values  $\leq 0.05$  indicate a statistically significant amount of the variance in the distribution of that species is explained by that treatment (edge effect or boundary type).

SPECIES	SOURCE OF VARIATION	SS	df	MS	F	P-value
Coachella Valley fringe-toed lizard	Edge Effect	11.569	6	1.928	1.629	0.150
	Within Group (Error)	91.107	77	1.183		
Flat-tailed horned lizard	Edge Effect	1.549	6	0.258	9.545	0.007
	Boundary Type	0.319	1	0.319	11.810	0.014
	Error	0.162	6	0.027		
Sidewinder	Edge Effect	0.008	6	0.001	0.585	0.735
	Boundary Type	< 0.0001	1	< 0.0001	0.010	0.923
	Error	0.014	6	0.002		
Shovel-nosed snake	Edge Effect	0.109	6	0.018	2.073	0.198
	Boundary Type	0.005	1	0.004	0.550	0.486
	Error	0.053	6	0.009		
Round-tailed ground squirrel	Edge Effect	0.075	6	0.013	1.345	0.364
	Boundary Type	0.197	1	0.197	21.085	0.004
	Error	0.056	6	0.009		
Desert kangaroo rat	Edge Effect	2.683	6	0.447	15.529	0.002
	Boundary Type	3.323	1	3.323	115.400	< 0.0001
	Error	0.173	6	0.029		
Harvester ants	Edge Effect	8.789	6	1.465	1.890	0.229
	Boundary Type	13.114	1	13.114	16.921	0.006
	Error	4.650	6	0.775		

Table 3. Results of linear regressions, with species abundance as the dependent variable and two habitat metrics as independent variables, included here as two separate one-variable models and together as a two-variable multiple regression model. Regression coefficients,  $R^2$ , and p-values are included.

Species		Edge distance	Sand compaction	Edge distance and sand compaction
Flat-tailed horned lizard	p	< 0.0001	< 0.0001	< 0.0001
	$R^2$	0.345	0.127	0.406
	Regression Coefficient	0.003	-0.241	.003/-0.16
Desert kangaroo rat	p	0.04	0.952	0.108
	$R^2$	0.038	< 0.0001	0.04
	Regression Coefficient	0.003	-0.669	0.001/-0.643

### Figure Captions

Figure 1. Satellite image depicting distribution of plots, extent of aeolian sand habitat, juxtaposition of suburban golf course development and abandoned agricultural fields, and roads

Figure 2a-2h. Mean counts and one standard error (indicated by the error bar) of species occurring on sand dunes and sand hummocks in the Coachella Valley at various distances from an anthropogenic habitat edge. Data for each year are the combined means for the plots on which the species occurred, with six repetitions per transect per plot. Data collected at >500 m represent the combined core plots.

Figure 3. Mean counts and one standard error (indicated by the error bar) of flat-tailed horned lizards at distances from two boundary types. Solid black bars represent data summarized from three plots adjacent to a four-lane road, with curbs, bounded by a suburban golf course community. Diagonally lined bars represent data summarized from five plots adjacent to a two-lane curbless road, bounded by abandoned agricultural fields and tree-row windbreaks. Both summaries include data combined from 2002 and 2003. Data for each year are the combined means for the plots on which the species occurred, with six repetitions per transect per plot.

Figure 1.

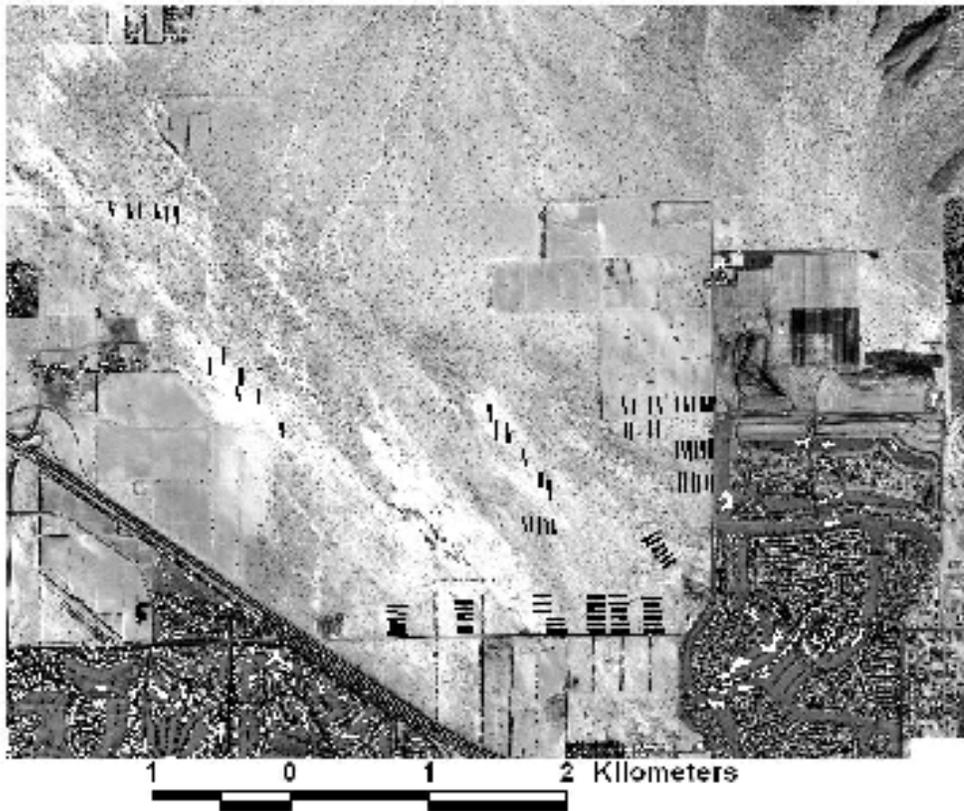


Figure 2a.

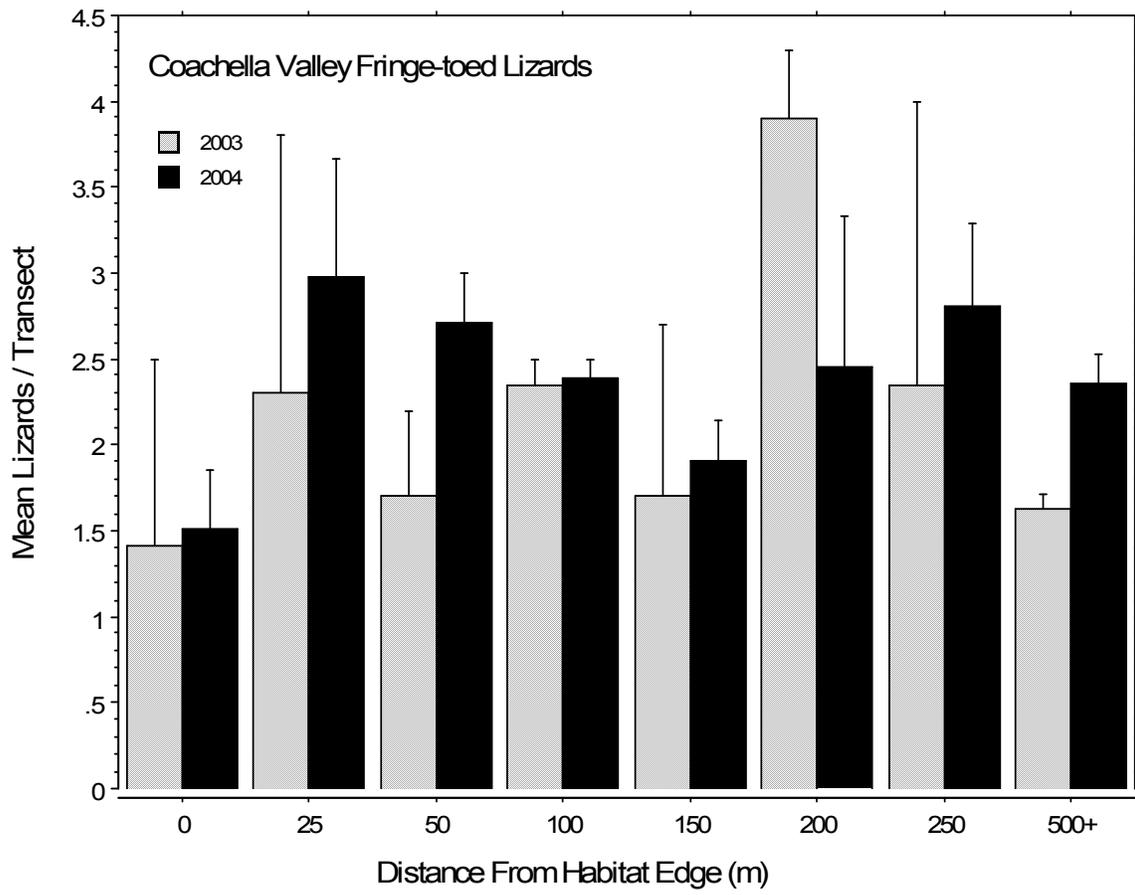


Figure 2b.

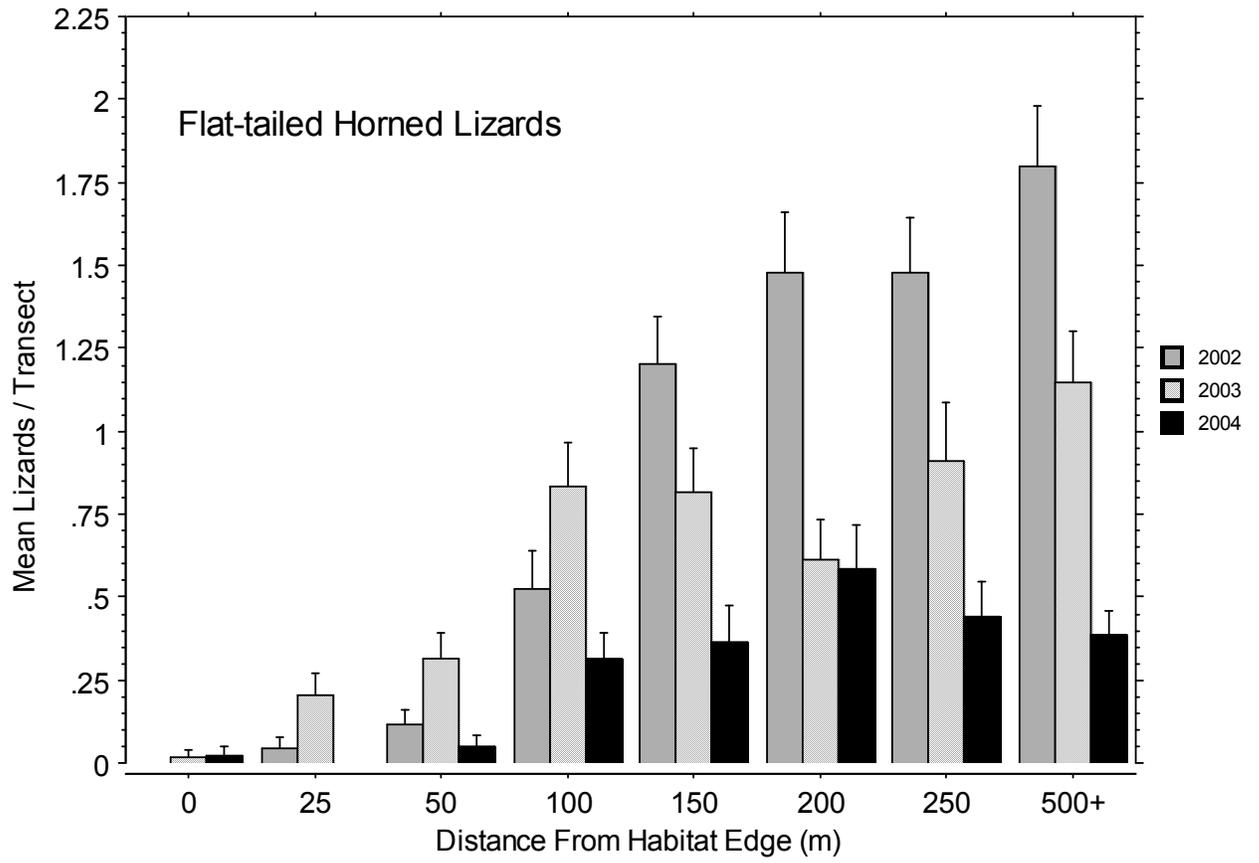


Figure 2c.

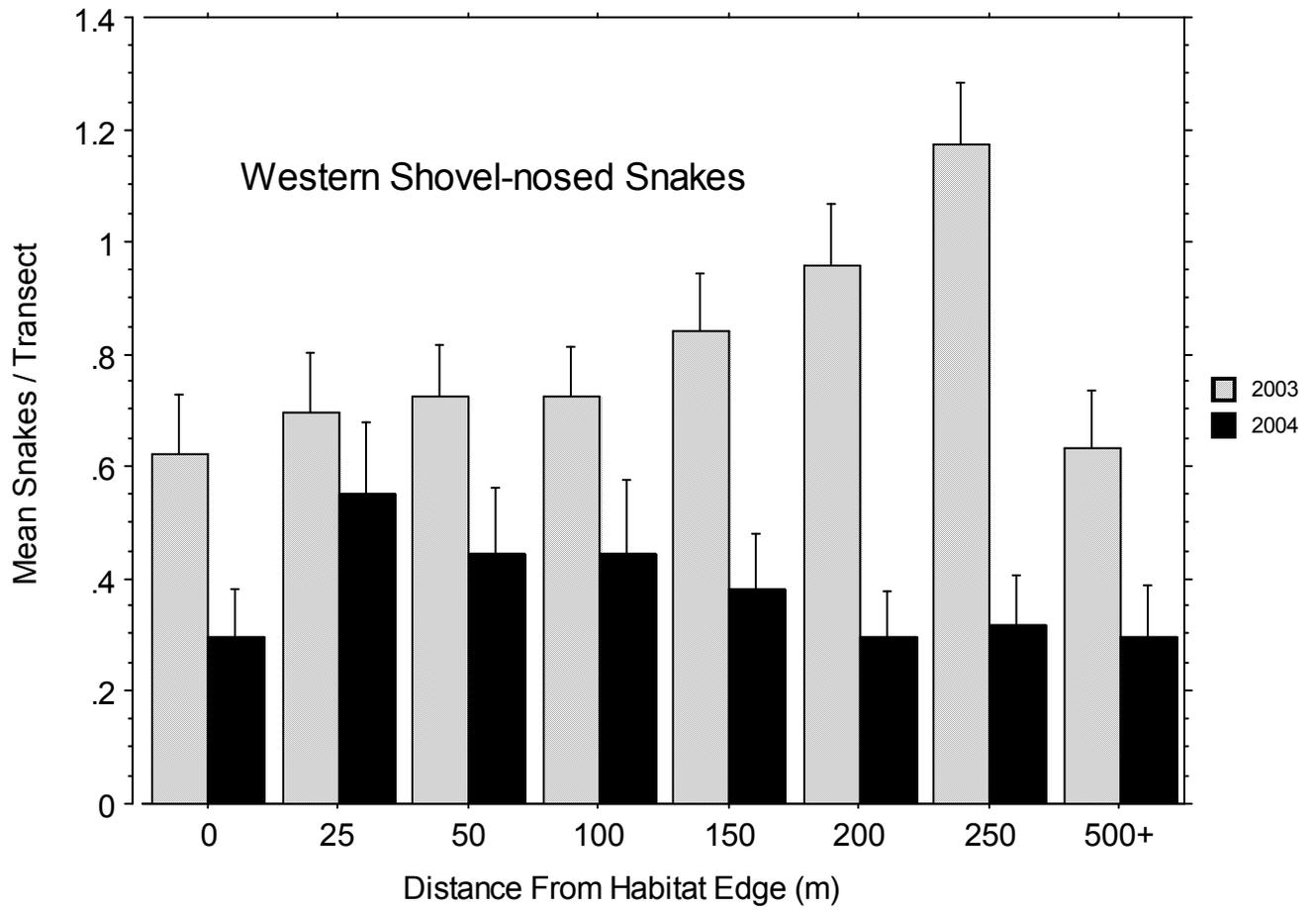


Figure 2d.

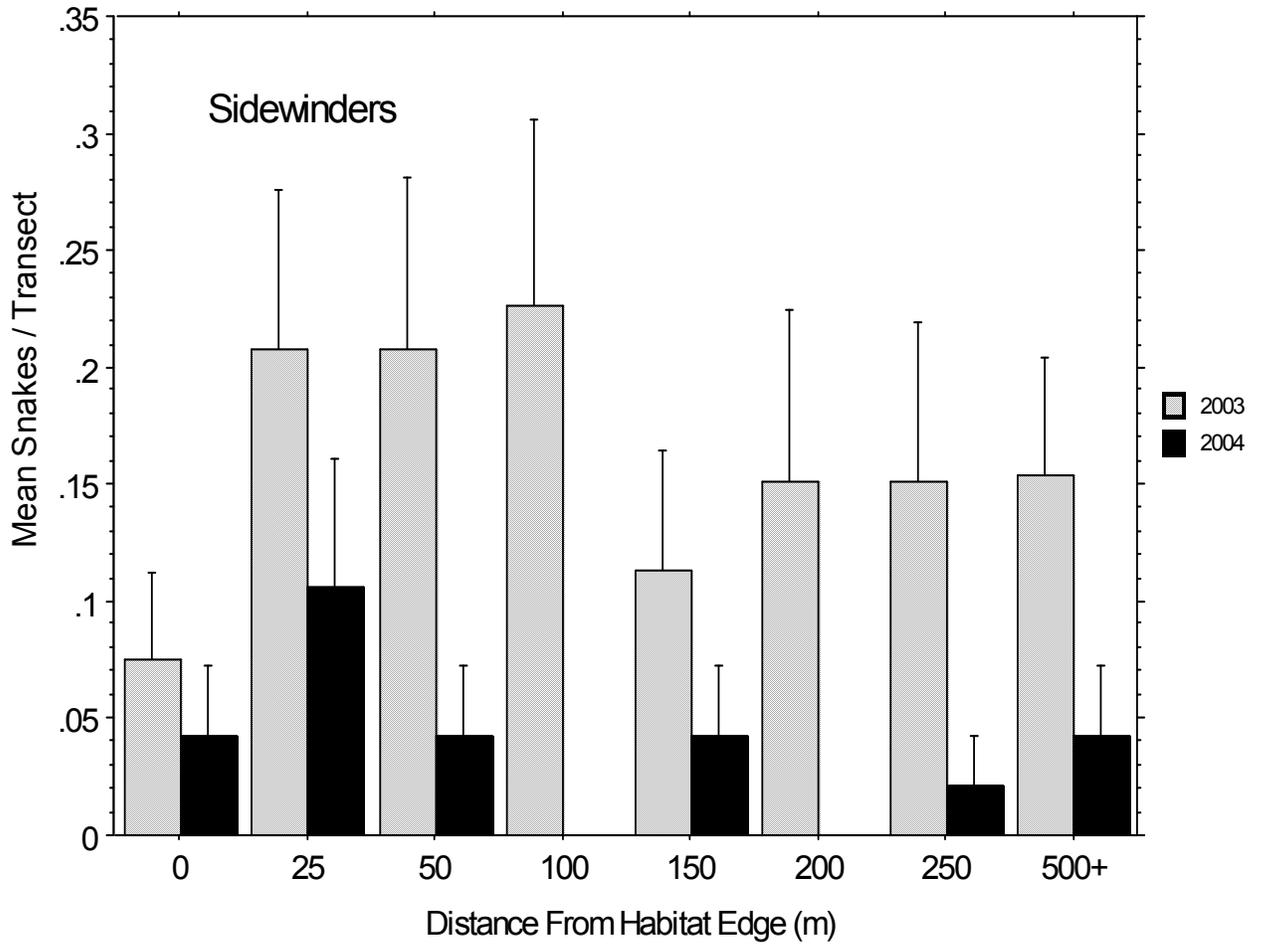


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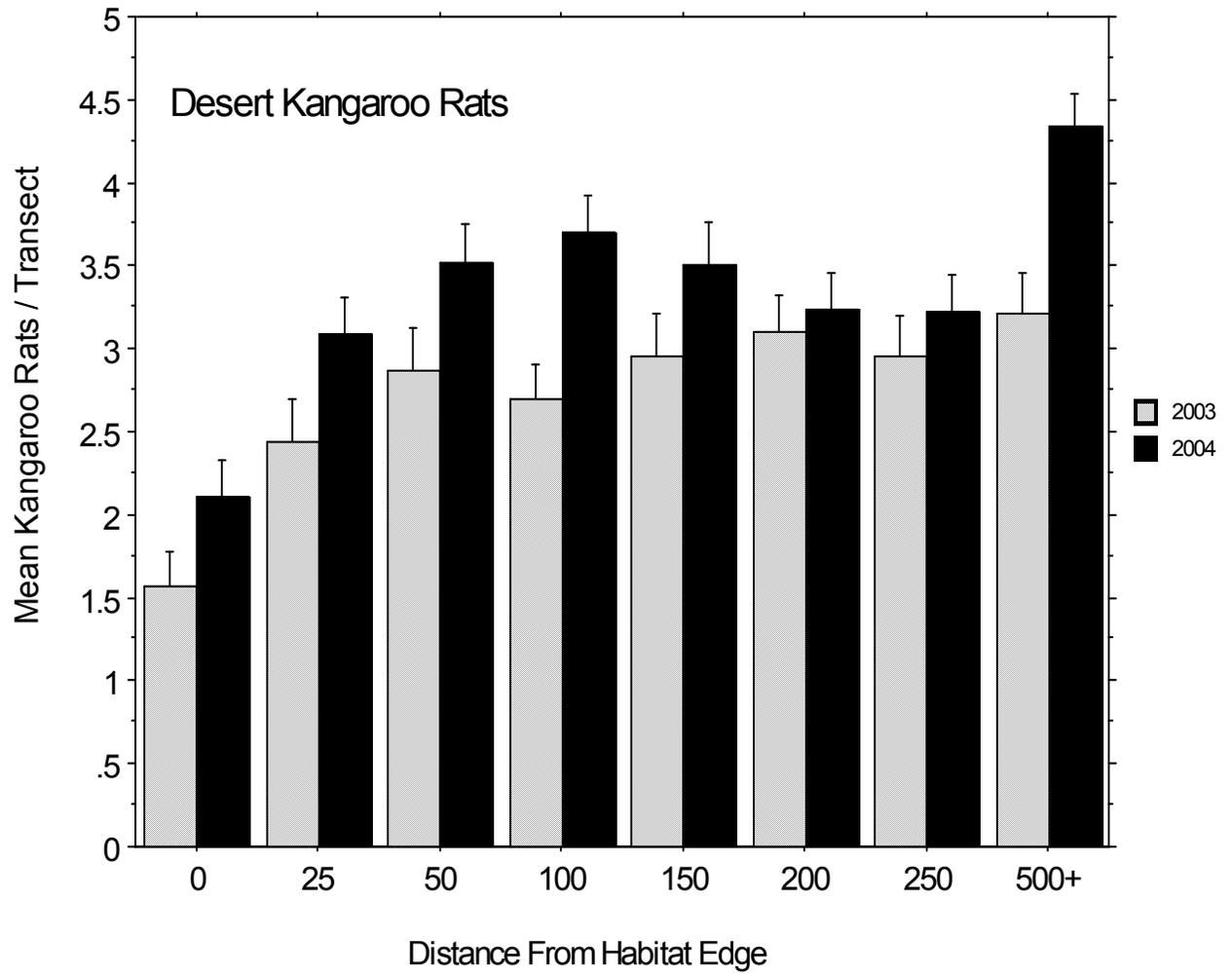


Figure 2f.

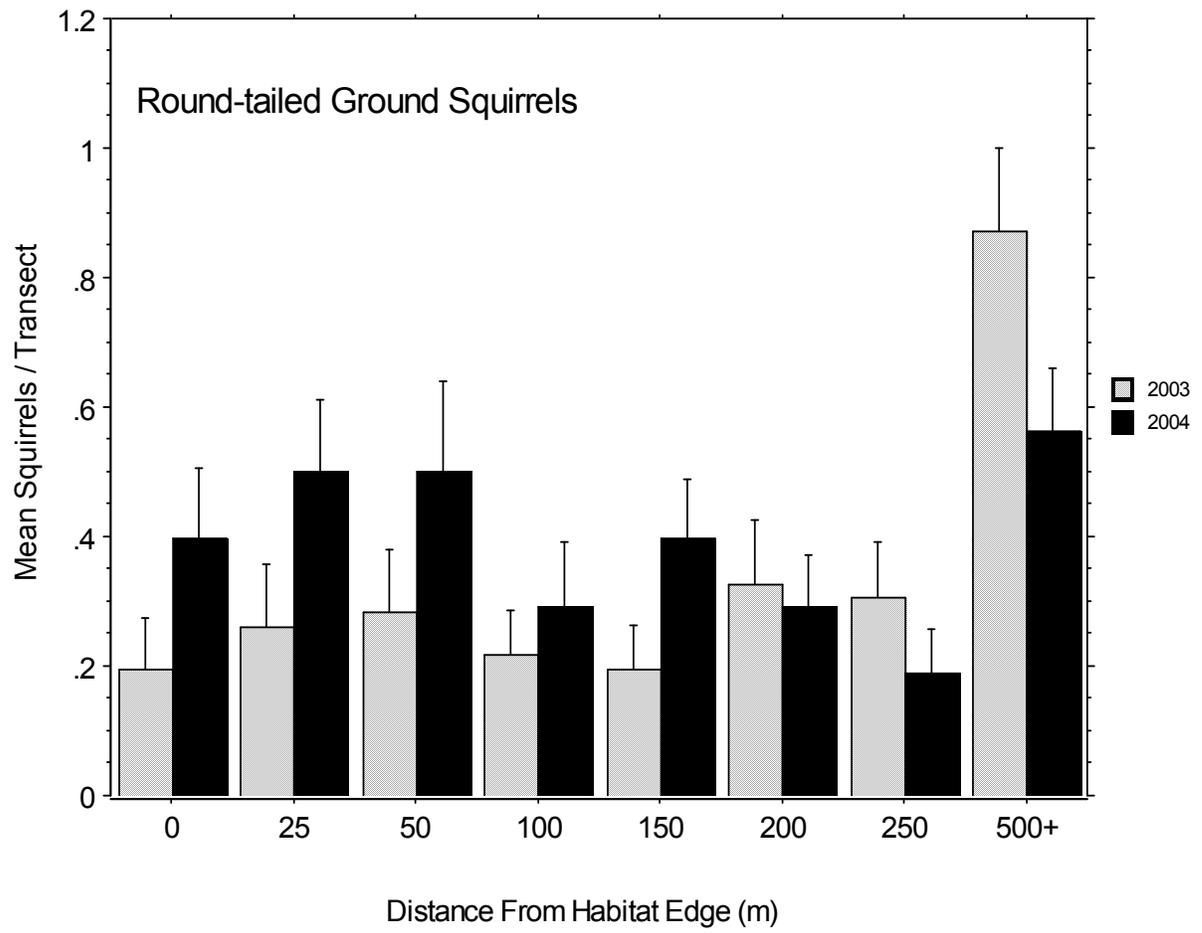


Figure 2g.

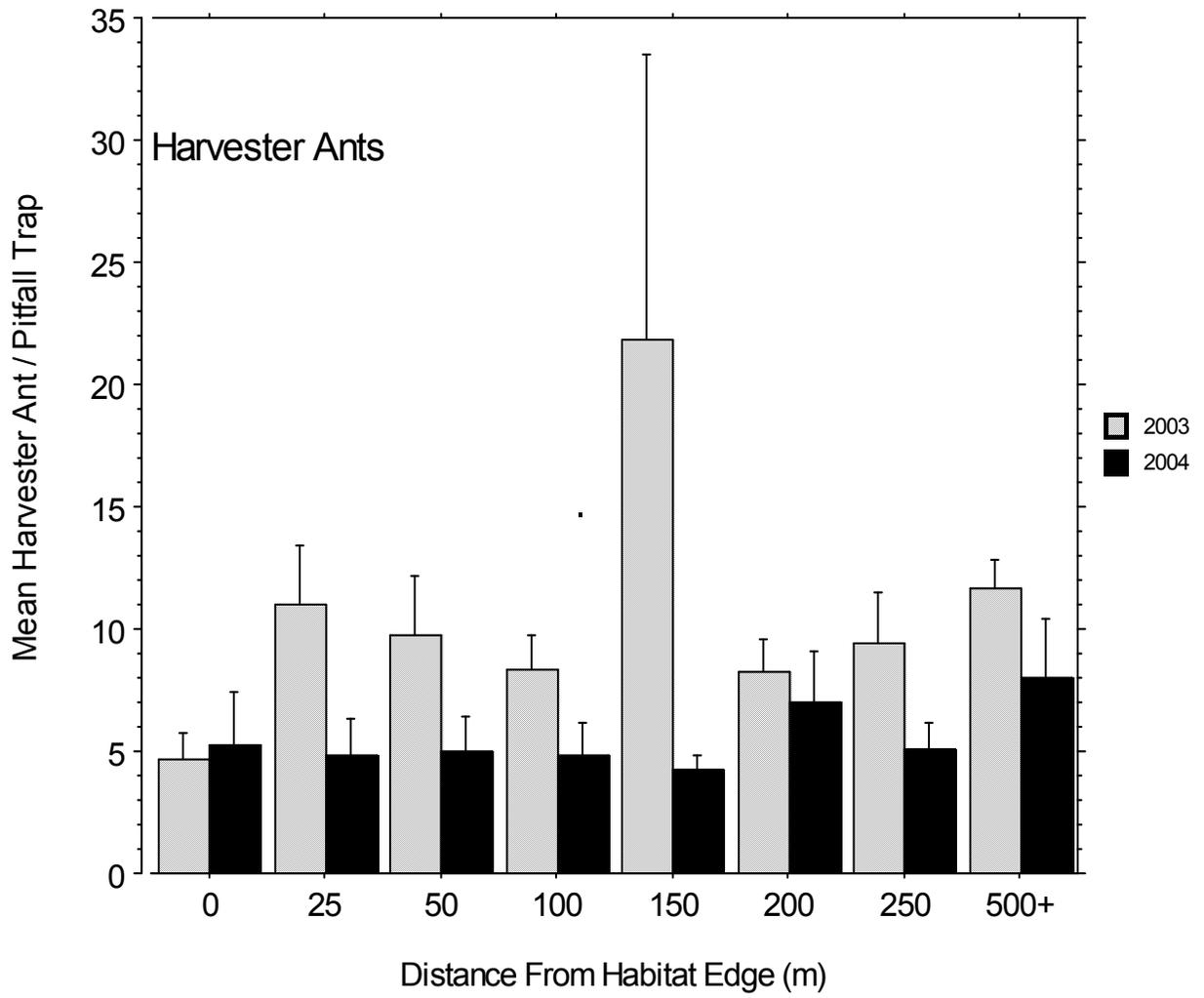


Figure 3.

