

HABITAT RELATIONSHIPS OF THE COACHELLA VALLEY FRINGE-TOED LIZARD (*UMA INORNATA*)

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ABSTRACT—The threatened Coachella Valley fringe-toed lizard (*Uma inornata*) is protected within a series of sand dune remnants. Understanding the specific habitat needs of these lizards is important to the management of this ecosystem. I examined habitat selection of *U. inornata* at both multiple isolated dunes and, more intensively, at a single dune site. For the multiple sites analysis, I found that habitat area and sand compaction were the most important features distinguishing between occupied and unoccupied dunes. At the single dune, I found sand compaction and the presence of plants such as *Dicoria canescens*, *Atriplex canescens*, and *Salsola tragus* to be associated with areas of high lizard use. The relative contribution of each of these variables differed with year, season, and age class of the lizards. In each year, including my multiple sites analysis, sand compaction was consistently the most important habitat characteristic I measured. *Uma inornata* were associated with locations on the dunes with deep, loose sand.

Fringe-toed lizards (*Uma* spp.) are restricted to aeolian sand habitats in the deserts of southwestern North America (Stebbins, 1944; Norris, 1958). In the Coachella Valley of southern California, limited distribution of aeolian environments, in conjunction with habitat loss due to regional dune stabilization and urbanization, has resulted in the listing of *U. inornata* as Threatened by the U.S. Fish and Wildlife Service in 1980. Subsequently, a preserve system has been established to conserve and maintain sand dune remnants. However, there are concerns about the long term viability of natural processes that maintain the aeolian habitat at one location in the preserve system (Barrows, 1996). Active management of sand dune habitat may ultimately be required to mimic the natural processes that would otherwise maintain this habitat. Consequently, an understanding of the habitat features important to these lizards is a necessary prerequisite to habitat manipulation.

Within aeolian habitat the distribution of *U. inornata* can be patchy (Turner et al., 1984). Previous studies have focused on the importance of sand grain size to lizard distribution within a site (Stebbins, 1944; Norris, 1958; Pough, 1970; Turner et al., 1984). Norris (1958) mentioned the potential importance of sand compaction and Turner et al. (1984) incorporated sand compaction, sand grain size,

and surface coarseness into a regression model that explained 81% of the variation in lizard densities. I built on these previous studies by investigating further the importance of sand compaction and considering also the distribution and density of plants.

I examined habitat selection at two scales. At a coarse scale I measured the relationship of habitat variables to the presence or absence of lizards at multiple sites. At a much finer scale I investigated features that explained the distribution of lizards at a single site. Together these data provide evidence of the features that are important to the distribution of *U. inornata*.

MATERIALS AND METHODS—I collected all data within the Coachella Valley, Riverside County, California. In 1993, I surveyed 20 isolated aeolian sand drifts (sensu Norris, 1958) and dunes in the Indio Hills on the northern edge of the valley and on Garnet Hill at the western end. In addition I studied one of the largest of these sites in detail in 1994 and 1995.

At isolated dunes I compared habitat variables at sites occupied ($n = 10$) by *U. inornata* to those at unoccupied sites ($n = 10$). All variables were tested for normality with a Lilliefors test (Lilliefors, 1967), and when necessary, corrected with appropriate transformations. I used independent t -tests to identify significant differences between occupied and unoccupied sites. I then used discriminant functions

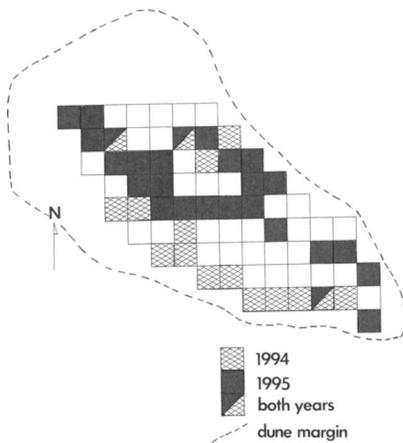


FIG. 1.—Distribution of high use areas by *Uma inornata* in 1994 and 1995. High use is defined here as use within grid cells that exceeded the overall plot mean.

analysis to identify which habitat variables could be used to discriminate between occupied and unoccupied sites.

At all 20 sites I selected a random starting point and stretched a 30-m tape along the slope contour. I surveyed a single transect on sand drifts less than 7,000 m² and two transects on drifts larger than 7,000 m². I measured vegetative cover using a line-intercept method (Mueller-Dombois and Ellenberg, 1974). I recorded the intercept lengths of live shrubs to the nearest 0.01 m and used the percent cover of all live plant species, as well as open sand, to compare occupied with unoccupied dunes.

For substrate analyses, I measured sand compaction at five points chosen randomly along each transect by dropping a metal spike (150 g, 25 cm by 1 cm) from a height of 1 m and recording the mean penetration (to the nearest 0.5 cm) of five drops. I measured sand grain size distribution using a separation sieve on a 200 to 350-g sample from each transect.

To determine presence or absence of *U. inornata* I visited each site at optimal time and weather conditions: during May, June and July, between 0900 h and 1200 h, with temperatures (unshaded, 1 cm above sand) between 33°C and 43°C. To survey a sand patch I traversed the site systematically, tapping all vegetation to flush lizards. While conclusive proof of the lizard's absence is impossible, I considered them absent if none were located after five visits (about five man-hours).

At a single isolated dune I compared *U. inornata* distribution with the occurrence of plant and substrate types. I overlaid a grid of 73 cells, each 10 by 10 m, in the center of the 1.3-ha dune (Fig. 1). I mapped *U. inornata* sightings within the grid on 60

days in 1994 and 67 days in 1995. As with the multiple-site surveys, I visited all sites during optimal time and weather conditions to insure high lizard activity.

I sampled vegetation by counting individual plants of each species in each cell. The timing and quantity of precipitation differed between years; nearly three times as much rain fell in 1995 than in 1994 (11.2 versus 3.9 cm). I surveyed vegetation in May 1994 and in both May and August 1995, as vegetative cover changed substantially from spring to summer months.

I measured sand compaction within each cell in May 1994 and in both May and August 1995, as higher rainfall was accompanied by stronger winds, which changed the dune's topography during the sampling period. Since I measured sand grain size at this site in 1993, and found all measurements within the preferred ranges previously published for *U. inornata* (Stebbins, 1944; Norris, 1958; Pough, 1970), this variable was not measured in subsequent years.

To identify habitat features that characterize high use areas for *U. inornata*, I followed Rice et al. (1986), Rotenberry (1986) and Welsh and Lind (1995) in using a combined statistical approach to create a habitat model, allowing cross-validation between methods. In the first method, I used step-wise multiple regression to determine which variables significantly contributed to explaining the variance in lizard distribution. In the second method, I used discriminant functions analysis to identify which variables differentiate two groups of lizard use categories. Since I was interested in identifying variables associated with high use areas by the lizards, the two groups I contrasted were those cells with lizard occurrences at or below the overall grid mean (low use) and above the grid mean (high use). Prior to inclusion in the discriminant functions analysis, all variables were tested for normality (Lilliefors, 1967) and transformed if necessary. I used SYSTAT 5.0 (Wilkinson, 1990) for all statistics.

RESULTS—Descriptive statistics for variables used to distinguish between occupied and unoccupied isolated sand habitats are shown in Table 1. Only habitat area and sand compaction differed significantly. I used discriminant functions analysis to determine if these two variables in aggregate could distinguish between occupied and unoccupied sites. The distinction was significant (Wilks' Lambda = 0.44, $F = 10.96$, $d.f. = 2, 17$, $P = 0.001$) and correctly classified 18 of 20 sites as occupied or unoccupied.

In 1994 I recorded 369 adult and 61 hatch-

TABLE 1—Summary statistics and *t*-test results for habitat variables measured on 20 isolated patches of aeolian sand in 1993. Degrees of freedom for all *t*-tests = 18.

	Occupied sites (<i>n</i> = 10)			Unoccupied sites (<i>n</i> = 10)			<i>t</i>	<i>P</i>
	Mean	1 <i>SD</i>	Range	Mean	1 <i>SD</i>	Range		
Habitat patch size (m ²)	6,900	6,350	900–20,000	1,300	1,600	120–5,000	3.55	0.002
Sand compaction (cm)	11	3	8–15	8	3	5.5–14	3.37	0.003
Open sand (%)	71	6	61–78	68	14	48–86	1.13	0.272
Live shrubs (%)	12	7	6–29	11	9	0–30	-0.11	0.912
Modal sand grain size (mm)	0.250	0.078	0.180–0.355	0.355	0.051	0.250–0.355	-1.44	0.171

ling *U. inornata* locations on a single isolated dune; in 1995 I recorded 434 adult and 167 hatchling *U. inornata* there. Habitat variables were used in a step-wise multiple regression to determine their relative and aggregate importance in explaining the occurrence of *U. inornata* within this site (Table 2). Pairwise correlations between variables were examined; all of the variables used in the regression models were independent. In 1994 and in summer 1995, sand compaction was the leading variable in explaining adult lizard distribution, accounting for nearly 35% of the variance in 1994 and 25% in summer 1995. Habitat selection in 1995 increased in complexity with the addition of vegetation variables to the habitat model. In aggregate, these variables accounted for nearly 50% of the variance in adult lizard distribution. In spring 1995, adult lizards were associated with spring Russian thistle (*Salsola*

tragus) and summer *Dicoria canescens*. Hatchling (young of the year) *U. inornata* in summer 1995 were associated with similar habitat features as were spring adults, even though most Russian thistles were dead when hatchlings first emerged in summer. Hatchlings associated negatively with living Russian thistle during summer months.

The discriminant functions analyses identified a similar, but not identical, set of habitat variables in creating a habitat model (Table 3). In 1994 the only difference from the step-wise multiple regression model was the addition of *Dicoria* as a feature that differentiated between high and low use areas for adult lizards. In spring 1995, none of the habitat variables I measured differentiated between high and low lizard use cells. In summer 1995, spring densities of *Salsola*, summer *Dicoria* densities and sand compaction separated high and low use

TABLE 2—Step-wise multiple regression models describing the contribution of habitat variables to explaining variances in *U. inornata* distribution on a single dune. Numerical values shown are correlation coefficients for variables after entry into the regression model. Numbers in parentheses are the order in which the variables were entered into the regression model. Coefficients shown in bold type are those variables which were also identified in the discriminant functions analysis procedure as associates of high lizard use areas.

Variable	Adults 1994	Hatchlings 1994	Adults 1995 (spring)	Adults 1995 (summer)	Hatchlings 1995
<i>Atriplex</i> (spring)	—	0.302 (2)	—	—	0.370 (3)
<i>Dicoria</i> (summer)	—	—	0.121 (2)	0.242 (3)	0.196 (2)
<i>Salsola</i> (spring)	—	—	0.052 (1)	—	0.103 (1)
<i>Salsola</i> (summer)	—	—	—	0.510 (2)	-0.258 (4)
Sand compaction	0.348 (1)	0.154 (1)	—	0.265 (1)	—
Multiple <i>R</i> ²	0.348	0.282	0.193	0.484	0.284
Probability (<i>F</i> test)	<0.001	0.001	0.001	<0.001	<0.001

TABLE 3—Single and multivariate probabilities for the contribution of habitat variables in discriminating between grid cells with high lizard use (above plot means) and low use (at or below the plot mean), using discriminant functions analysis. Probabilities shown in bold type are those variables also identified as explaining a significant amount of the variance in *U. inornata* densities in the stepwise multiple regression model.

Variable	Adults 1994	Hatchlings 1994	Adults 1995 (spring)	Adults 1995 (summer)	Hatchlings 1995
<i>Atriplex</i> (spring)	—	0.010	—	—	—
<i>Dicoria</i> (summer)	0.003	—	—	0.001	—
<i>Salsola</i> (spring)	—	—	—	0.013	0.006
<i>Salsola</i> (summer)	—	—	—	—	—
Sand compaction	<0.001	0.002	—	0.001	0.002
Wilks' lambda	0.600	0.786	0.862	0.542	0.800
F-statistic	<0.001	0.003	0.269	<0.001	0.061

areas for adult lizards. For hatchlings that year, spring Russian thistle densities and sand compaction discriminated between use groupings. Habitat attributes for cells with higher than average lizard use are shown in Table 4.

DISCUSSION—Within the landscape mosaic of aeolian sand there are large areas of suitable sand size where *U. inornata* is nonetheless patchy in distribution. Previous studies have indicated that these lizards require sand grains between 1.0 and 0.1 mm in diameter, with preferred modal sizes being: less than 0.5 mm (Stebbins, 1944); 0.375 mm to 0.11 mm (Norris, 1958); and 0.5 mm to 0.25 mm (Pough, 1970). All of the sites investigated in this study, occupied and unoccupied, had modal sand grain sizes within the range of those reported to be preferred by *U. inornata*. Since sand grain size alone did not explain the presence, ab-

sence, or abundance of *U. inornata* in aeolian habitats, other features also must contribute.

Results of the multiple-sites survey indicated that sand compaction and sand patch size were important habitat features for the lizards. The discriminant functions analysis correctly classified all but two of the 20 sites using those two variables. One of those classified incorrectly as occupied, when in fact it was not, was occupied by *U. inornata* in the 1980's (Allan Muth, pers. comm.), suggesting a recent extirpation. The coarse nature of my data prevented any conclusions about the importance of vegetative features.

At the single dune where I conducted more intensive investigations, the combined use of step-wise multiple regressions and discriminant analyses allowed me to validate variables within an *U. inornata* habitat model. Sand compaction, along with four-winged saltbush (*Atriplex*

TABLE 4—Habitat values for grid cells with high lizard use (above the overall plot average) for those variables that contributed significantly to discriminating between high and low *U. inornata* use areas using a discriminant functions analysis habitat model.

Variable	<i>Atriplex</i> (Sp)			<i>Dicoria</i> (Su)			<i>Salsola</i> (Sp)			Sand compaction		
	Mean (/m ²)	1 SD	Range	Mean (/m ²)	1 SD	Range	Mean (/m ²)	1 SD	Range	Mean (cm)	1 SD	Range
Adults 1994	—	—	—	0.04	0.05	0.00–0.16	—	—	—	9.5	2.5	6.0–13.5
Hatchlings 1994	0.042	0.05	0.00–0.18	—	—	—	—	—	—	9.5	2.5	6.0–13.5
Adults 1995 (summer)	—	—	—	0.082	0.07	0.00–0.22	0.242	0.15	0.02–0.58	9.0	1.5	6.0–13.0
Hatchlings 1995	—	—	—	—	—	—	0.232	0.14	0.03–0.58	9.0	1.5	7.0–13.0

canescens), Russian thistle and *Dicoria* densities were confirmed as features that distinguished lizard high use areas in both statistical techniques. The relative contribution of each of these variables varied with year, season, and age class of the lizards.

In each year, including my multiple-sites analysis, sand compaction was consistently the most important habitat characteristic I measured. *Uma inornata* were associated with locations on the dunes with deep, loose sand. Turner et al. (1984) identified sand compaction as important to explaining differences in lizard densities among sites. Fringe-toed lizards bury in loose sand to escape predators and hot temperatures (Stebbins, 1944; Pough, 1970). Burying is insufficient to escape the highest summer temperatures at unshaded locations; by midday, lethal temperatures reach the depths at which *U. inornata* normally bury. Before the onset of lethal temperatures, buried lizards emerge and either enter rodent burrows, or sit or bury in the shade of dense shrubs (Pough, 1970).

Beyond providing shade for cooling, shrubs are an important food resource. I regularly observed *U. inornata* eating *Dicoria* leaves, gleaning arthropods from the foliage and excavating insect larvae from the plant base. Though not as often, I did see the lizards gleaning insects from Russian thistle leaves as well. Both of these plant species appeared to have much greater arthropod abundances than did perennial shrubs such as the saltbush. When annual plants were common, as in 1995, *U. inornata* were associated with areas of high *Dicoria* or Russian thistle densities. I believe there is a critical maximum density for these plants; above this density lizards avoid the area, but this avoidance was not observed here.

Russian thistle was the only non-native, invasive plant on my plot. Land managers have expressed concern that this species may have a negative impact on *Uma inornata*, and thus may need to be controlled. My data indicate that Russian thistle can be a positive component of fringe-toed lizard habitat. *Dicoria* (a native) and Russian thistle have a similar appearance and distribution when occurring on aeolian sands. Important differences do exist: Russian thistle is generally dead by mid summer and is not eaten by *U. inornata*; *Dicoria*, which they do eat, persists through late summer, and

flower typically in October. Durtsche (1995) identified *Dicoria* as an important food plant for *U. inornata* in late summer and suggested that this plant's abundance may be related to *U. inornata* population trends.

The seasonal differences in plant associations between adult and hatchling *U. inornata* may be explained by differences in the lizards' risk of predation. In addition to all the same predation pressures the adults face, hatchlings are also subject to predation from adult lizards of several species, including their own (Allan Muth and Mark Fisher, pers. comm.). Hatchling *Uma* appear to seek dense vegetation for cover, whether or not it has abundant food resources, and the hatchlings avoid areas of high adult use such as live Russian thistles in late summer. Dead Russian thistle in summer, (characterized as spring *Salsola* in this report), as well as saltbush have low food resources but high cover.

These data in aggregate explain only a portion of the variance in adult lizard distribution in 1994 and 1995. Social interactions (breeding and antagonistic behaviors) may not be related to habitat features and thus may account for much of the unexplained variance. The lack of habitat correlates to lizard distribution in spring 1995 may reflect the relatively intense breeding activity occurring at that time. Temporary food resources also affect lizard distribution. For example, episodic mating swarms of small flies resulted in several individual lizards foraging together, away from their regular areas of occupancy. Although the swarms lasted from only a few hours to a few days, nevertheless they affected lizard distribution.

The associations described here should provide important information to land managers if habitat manipulation is necessary to manage aeolian habitat within the established preserve system. The site I studied intensively for two years is within the preserve where there are concerns about the viability of natural processes that maintain the habitat (Barrows, 1996). I believe it is representative of the area where habitat manipulation may be necessary.

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