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Dry Season Habitat Use by Lizards in a Tropical Deciduous Forest of Western Mexico

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Tropical deciduous or dry forests are characterized by strong seasonality in precipitation, typically having a prolonged dry season lasting at least four months (Bullock, 1986; Murphy and Lugo, 1986). As the dry season progresses, the forest canopy changes from a relatively homogeneous dense cover of the wet season to a more variable and open canopy (Lott et al., 1987; Bullock and Solis-Magallanes, 1990). As deciduous trees lose their leaves, more sunlight penetrates the canopy and creates a variety of forest gaps and thermal microenvironments on or near the ground. In contrast, forest habitat near seasonally dry watercourses (arroyos), remains green throughout the dry season, providing shaded habitats with dense canopy cover (Lott et al., 1987; Bullock and Solis-Magallanes, 1990).

The dry season in a tropical deciduous forest represents a challenging time of year for most ground dwelling vertebrates. Water and energy resources are at the yearly low (Janzen and Schoener, 1968; Lister and García, 1992), and thermal options may also be reduced, especially in the more shaded habitats of arroyos. Many vertebrates show reduced activity or seasonal changes in habitat use during the dry season (Beck and Lowe, 1991; Ceballos, 1995). Other species may move away from upland habitats and into arroyos or watercourses, which are used as dry season refuges (Ceballos, 1990). Those that remain active tend to be juveniles or adults of smaller species (Fleming and Hooker, 1975; Lister and García, 1992; Casas-Andreu and Gurrola-Hidalgo, 1993; Fitzgerald et al., 1999).

We know little about how dry forest lizards respond to seasonal changes in habitat structure or of the patterns of activity exhibited by lizards that remain active during the dry season. Our study examines how lizard habitat use and activity (i.e., species found to be active, timing, and amount of activity) are influenced by the variability in forest structure during the dry season in a tropical deciduous forest in southwest Mexico. We address the following questions: (1) During the dry season, does lizard activity differ between arroyo and upland habitats? (2) Is lizard activity related to forest canopy cover during the dry season? and (3) Do lizards show greater activity in closed forest or in more open habitats near edges or gaps?

Our study was conducted at the Estación de Biología Chamela (EBCH), a lowland tropical dry forest reserve in coastal Jalisco, Mexico, approximately 3 km from the Pacific coast (19°30′N and 105°03′W). Precipitation averages 748 mm/yr, 80% of which falls from July through October after a 7–8 month dry season spanning November to June (Bullock, 1986). Habitat at the station consists primarily of two vegetation types distributed along alluvial and moisture gradients (Bullock, 1986; Lott et al., 1987). Upland forests are dry-deciduous with well-developed understory and canopy 4–15 m in height. Arroyo forests contrast structurally and floristically with upland forests by having a relatively open understory and a taller evergreen semideciduous canopy (Lott et al., 1987). During the dry season, visibility through the understory is similar in both habitat types, even though arroyo habitats show greater canopy cover (see below).

Data were gathered during the dry season in late February and early March 1999. We assessed lizard activity in two ways: (1) time-constrained visual searches along transects; and (2) recording lizard trackways on sand plots (described below). We conducted time-constrained visual searches (Crump and Scott, 1994) along six 1-km transects on foot trails in each of the two habitat types. Transects were sampled at a pace of 2 km/h between 0800 and 1800 h. Each was sampled twice over the course of the study, and all transects were given equal search time totaling 120 search hours. Each lizard observed was treated as an independent sample, even though it was possible that some individuals were seen more than once (at different times) on our transects. We recorded sightings of five species: *Anolis nebulosus, Ameiva undulata, Cnemidophorus communis, Cnemidophorus lineatissimus*, and *Sceloporus utiformis*. To minimize bias caused by variation in visibility of species and among transects, we recorded observations only within 3 m on each side of the transect. For each observation, we recorded the species and time of day. Species identifications were based on published accounts (García and Ceballos, 1994) and from EBCH reference collections. If a lizard could not be identified with certainty, it was recorded as unknown.

To assess lizard activity on a finer scale, and to further explore the effect of canopy cover and forest gaps on lizard activity, we set up 1-m^2 plots dusted with fine sand (sand plots). These sand plots allowed us to monitor tracks left by lizards in the forest. We arranged 24 sand plots at sites adjacent to each visual search transect, 12 in uplands and 12 in arroyos. Sand plots were paired at each site; one in the open (canopy gap) and the other in denser forest and placed a minimum of 10 m apart. The plots were cleared early each morning and the number of new lizard trackways was recorded at the end of each day for 12 days. We used a spherical densiometer to determine canopy cover at 10 sites spaced approximately 100 m apart on each transect. For each of those sites we took the mean of four canopy cover measurements, one for each cardinal direction.

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TABLE 1. Observations of lizard activity during 120 search hours along six 1-km transects (three in upland habitats; three in arroyo habitats) during the dry season in a tropical deciduous forest in western Mexico. The five species were not found active in the same proportions in the two habitat types. Only lizards identified to species were included in the analysis.

Species	Habitat type	
	Uplands	Arroyos
Anolis nebulosus	55	18
Ameiva undulata	1	11
Cnemidophorus communis	63	33
Cnemidophorus lineatissimus	189	95
Sceloporus utiformis	246	31
Unidentified	145	34
Totals	699	222

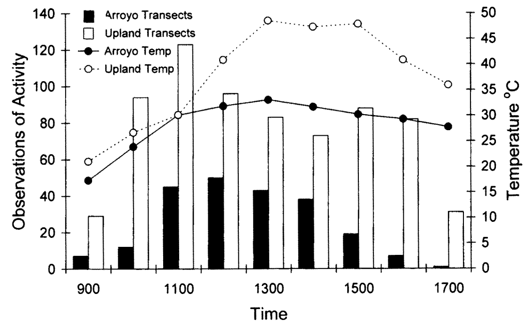

FIG. 1. Hourly distribution of lizard activity ($N = 921$) compiled from 120 visual search hours along six 1-km transects (three in upland; three in arroyo habitats) during the dry season in a tropical deciduous forest in western Mexico. Circles indicate mean air temperatures (shade) at 1.5 m above the ground taken at 10-min intervals on a typical day in early March. We saw significantly more lizards on upland than arroyo transects. In addition, lizards in upland habitats showed activity later into the afternoon than did those in arroyos.

We recorded surface temperatures every 10 min in upland and arroyo habitats with dataloggers (Onset Instruments©) throughout a typical day in early March. During our study, there was no precipitation and little variation in temperature among individual days. Daily highs during late February typically average near 30°C and daily lows average near 15°C (Bullock, 1986).

We used *G*-tests (Sokal and Rohlf, 1995) to test the hypothesis that lizard species were active in the same proportions in arroyos and uplands and that there was no difference in activity between the two habitat types. We used a *t*-test (paired by hour for arroyos vs. uplands) to test whether the number of observations of activity differed between the two habitat types. We used linear regression to determine the relationship between lizard activity and forest canopy cover, and a two-way ANOVA (SYSTAT, New Statistics, SPSS, Chicago, IL, 1997) to determine the effects of macrohabitat (arroyo vs. upland) and microhabitat (gaps vs. closed forest) on number of lizard trackways observed in the sand plots.

We observed five species of diurnal, heliothermic lizards commonly active in the dry season (Table 1). All species except *A. undulata* were more frequently encountered in the uplands; however, the five species were not found in the same proportions in the two habitat types ($G = 70.4$, df $=4$, $P < 0.001$; Table 1). Adult individuals of *Cnemidophorus* were rarely seen; our sample includes > 90% juveniles. *Sceloporus utiformis* dominated our upland sample (44.4%), whereas *C. lineatissimus* dominated our arroyo sample (50.5%, Table 1).

Lizards were active from 0900 to 1800 each day in both uplands and arroyos, but in the upland habitats, lizard activity peaked significantly earlier and extended significantly later into the afternoon ($G = 60.96$, df $= 8$, $P < 0.001$; Fig. 1). Lizards in arroyos showed a narrower window of activity, mostly between 1000 and 1500 h, whereas lizards in upland habitats remained active later into the afternoon (Fig. 1). In the arroyos, lizard activity showed a peak between 1100 and 1200 h, the same time of day that surface temperatures were at their daily high. Lizard activity in upland habitats also showed a peak between 1100 and 1200 h; however, surface temperatures did not peak in upland forest until around 1400 h, a time when lizard activity actually decreased. After 1400 h, surface activity increased slightly in uplands as surface temperatures gradually cooled. Based on our datalogger readings, surface temperatures were generally over 10°C warmer in upland habitats than in arroyos between 1300 and 1600 h.

We saw nearly three times as many lizards active per 1-km transect in the uplands ($\bar{x} \pm$ SD = 233, $\pm$ 21.7) than in the arroyos (74, $\pm$ 44.3) and over three times as many lizards active per search hour in upland (11.7, $\pm$ 30.4) than in arroyo (3.7, $\pm$ 19.2) transects ($t = -6.9$, df $= 8$, $P < 0.001$; Fig. 1).

We found a significant negative relationship between canopy cover and lizard activity among the 1-km transects ($r = -0.94$, df $= 4$, $P < 0.01$; Fig. 2). This relationship was also significant at the microhabitat level: 1-m^2 sand plots in microhabitats with lower canopy cover showed more lizard trackways ($r = 0.72$, df $= 22$, $P < 0.01$). When sand plots in arroyos were analyzed separately from those in uplands, canopy cover remained negatively correlated with number of lizard trackways, but the relationship was not as strong for uplands as arroyo habitats ($r = -0.62$, $P < 0.05$; $r = -0.89$, $P < 0.01$ for uplands and arroyos respectively; see Fig. 3).

Sand plots situated in gaps (= edge microhabitats) contained significantly more trackways than those in forest habitats (two-way ANOVA, df $= 1$, $F = 10.2$, $P = 0.005$; Fig. 4). Interestingly, the mean number of lizard tracks/plot on the 24 sandplots did not differ significantly between uplands and arroyos ($F = 0.010$, $P = 0.92$; Fig. 4).

Our results show that, in tropical deciduous forest, lizard activity during the dry season is greater in upland forests and in microhabitats associated with forest gaps. Part of this pattern can be explained by differences in specific habitat preferences among the liz-

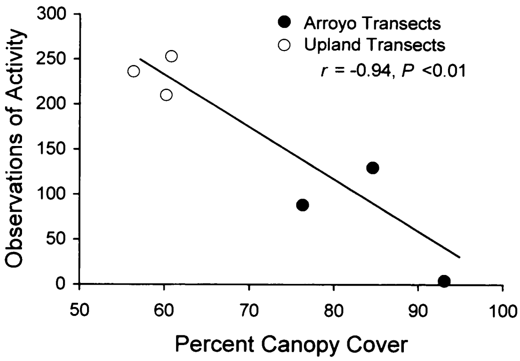

FIG. 2. Relationship between canopy cover and lizard activity observed during 120 search hours along six 1-km transects (three in upland habitats: three in arroyo habitats). For percent canopy cover, each point represents a mean of 10 evenly spaced cover measurements within each 1-km transect ($r = -0.94$, $P < 0.01$).

ard species we observed (see Casas-Andreu and Gurrola-Hidalgo, 1993; García and Ceballos, 1994). For example, *S. utiformis* may be more active in upland areas (Table 1) because it forages in the leaf litter, which is more abundant in uplands during the dry season (García and Ceballos, 1994). *Anolis nebulosus* shows greatly reduced activity during the dry season overall, switching from foraging in trees to foraging on the ground (Fleming and Hooker, 1975; Lister and García, 1992).

The primary explanation for differences in activity between habitat types is likely because of differences in thermal environments. During the dry season, upland habitats may remain warmer later in the day than do more densely forested arroyo habitats (Barradas, 1991; this study), which provide more thermal options for lizard activity (Fig. 1). In addition, upland forests on our study site varied in their degree of deciduousness on a local scale (tens of meters), probably in response to soil depth and moisture (see Lott and Bullock, 1987) to create a mosaic of variable thermal environments on the surface. Because they are more shaded, arroyo habitats may offer fewer thermal options for diurnal heliothermic lizards during the dry season and may constrain lizard activity to edge or gap microhabitats.

On a smaller scale (1-m^2 sand plots), lizards may respond more strongly to open habitats (i.e., gaps) in arroyo environments than they do in uplands, perhaps because openings in the canopy are more limited in arroyos. At this finer scale, lizard activity may be similar in both arroyo and upland habitats, but more activity is focused in gaps or openings within arroyo habitats (see Fig. 4). Because fewer trees lose their leaves during the dry season in arroyo habitats, open environments are more rare than in uplands. Lizard activity may thus be more restricted to forest gaps, and fewer lizards may be seen active overall in arroyo forest.

Others have shown that lizard abundance and activity can be strongly affected by forest gaps in tropical (Vitt et al., 1998) and temperate forests (McLeod

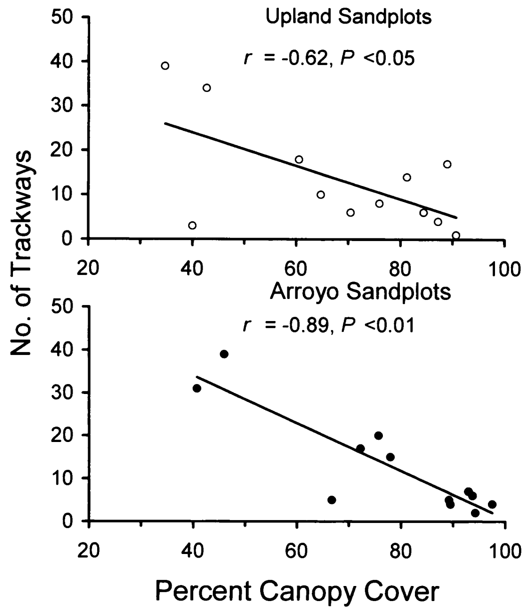

FIG. 3. Relationship between canopy cover and number of lizard tracks observed over 12 days on 1-m^2 sand plots in upland ($r = -0.62$, $P < 0.05$) and arroyo ($r = -0.89$, $P < 0.01$) habitats: each point represents one individual 1-m^2 sand plot.

and Gates, 1998). Daytime temperatures are warmer in gap/edge locations than forest, and heliothermic lizards tend to be more common in these habitats (Casas-Andreu and Gurrola-Hidalgo, 1993; Vitt et. al., 1998). Our results suggest, that during the dry season in tropical deciduous forest, heliothermic lizards are more active in gap/edge habitats than the more heavi-

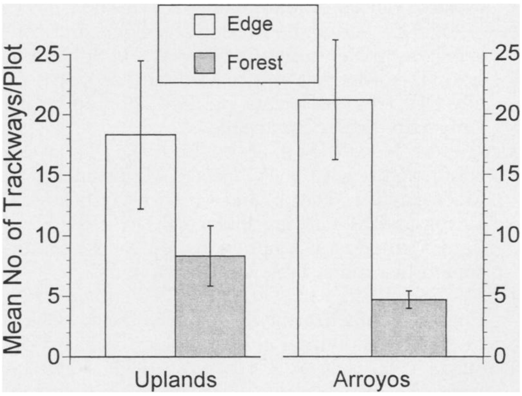

FIG. 4. Effect of edge habitat on observations of lizard activity (mean number of total trackways observed on each 1-m^2 sand plot over 12 days). Vertical lines represent ± 1 SE. Sand plots in gap (edge) microhabitats showed significantly higher lizard activity than did those placed in closed forest microenvironments. Number of trackways did not differ between upland and arroyo sand plots.

ly covered forest. Because of their greater deciduousness, upland habitats present a greater availability of gaps and may provide lizards with more thermal options to sustain activity during the dry season.

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The Tadpole of *Proceratophrys avelinoi* (Anura: Leptodactylidae)

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The genus *Proceratoprhys* is poorly known. It consists of 14 currently recognized species (Frost, 2000) of medium-sized frogs distributed from northeastern Argentina and Paraguay to southeast Amazonia (Rondonia State), eastern and southern Brazil. *Proceratophrys avelinoi* was described from Misiones, Argentina (Mercadal de Barrio and Barrio, 1993). The larval stage of this species is unknown. Herein, we describe the tadpole and the characteristics of the internal oral anatomy of *P. avelinoi* using scanning electron microscopy (SEM).

Proceratoprhys avelinoi tadpoles ($N = 6$) were collected at Estancia Hidromineral Santa Clara, Munic. Guarapuava, Paraná State, Brasil, in June 1998. The tadpoles were in a pond, about 5.0 cm deep; the surface of the pond was covered with aquatic vegetation. This pond was located about 100 m from the margin of the Jordão River. The specimens are deposited at the Museu de Historia Natural Capão da Imbuia, Curitiba, Paraná, Brasil, with number MNHCI 4198. Spec-

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