HABITAT SPECIFICITY IN THREE SYMPATRIC SPECIES OF AMEIVA (REPTILIA: TEIIDAE)

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Abstract. Three sympatric species of Ameiva in Costa Rica (A. quadrilineata, A. festiva, and A. leptophrys) were found in distinct habitats with respect to vegetation cover, ground insolation, environmental temperatures, surface litter, and activity periods.

Ameiva quadrilineata commonly forages in an area of open, low vegetation cover adjacent to bare soil. Its habitat is sunnier and warmer than those occupied by the other two Ameiva. A. festiva usually forages in the open edge of forests where somewhat lower percentages of ground are exposed to direct sunlight and there are lower environmental temperatures than in the habitat of A. quadrilineata. Its peak of foraging activity is later in the morning than is that of A. leptophrys. Adult A. leptophrys forage even deeper into the forest than the other two species where even less of the ground surface is insulated, the ground substrate temperatures are lower, and there is a higher percentage of ground litter. However, this species basks in the same area in which A. festiva forages, but earlier in the morning. Newly hatched A. leptophrys are found in an ecological habitat distinct from that of the adults, but very similar to that of adult A. festiva.

There appeared to be no differences in gut contents among the three species with respect to type of food items. However, A. quadrilineata contained slightly smaller sized food items than did the other two species. Body temperatures while foraging were very similar in all three species, but were maintained under very different sunlight conditions and microclimatic temperatures.

Three species of lizards of the genus Ameiva (Teiidae) occur sympathetically on the Osa Peninsula of Costa Rica. These are A. quadrilineata, A. festiva, and A. leptophrys (Taylor 1956). These species were studied within a 6-mile radius of Rincon de Osa, in the Province of Puntarenas, from July 26 to July 31 and September 1 to September 6, 1967. In a preliminary examination of these sympatric populations, considerable overlap of habitat was observed, suggesting a study for defining their specific habitat. Other studies have been conducted regarding habitat specificity of sympatric lizards in which differences such as temperature preferences and perching habits (Rubal 1961), temperature tolerances and activity periods (Hirth 1963), and specificity for certain plant associations and different foods (Milstead 1957) have been observed.

To determine differences in the specific habitat of the lizards in this study, the following aspects were chosen: habitat selection (with respect to vegetation cover, ground exposed to direct sunlight, and temperature), temperature preferences, activity periods, type of food eaten, and food size.

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Materials and Methods
Collecting equivalent amounts of information for the three species was difficult because Ameiva quadrilineata is more abundant in easily accessible areas than are the other Ameiva species. When Ameiva were located, the following information was recorded pertaining to the

Constant monitoring of site 1 was discontinued at 1930. Movements 8-11 were along the base of a steep slope.

14 July–29 October At 1545, 14 July, he was at site 31, at approximately the same elevation as site 1. At 1030, 15 July, he was at site 32. At 0950, 3 August, was at site 41 and at 1100, 3 September, was at site 51. On 14 October he was at site 61 (time not recorded). At 1730, 28 October, he was at site 71 and at 1100, 29 October, was at site 72.

This snake ranged over an area of 726 m². He returned to but one spot, and that only once.

Literature Cited


lizard and the area within a 3-m radius around it: species, time of day, type of activity in which the lizard was engaged (foraging, basking, or resting in the shade), a diagram of the immediate vegetation cover, per cent of cloud cover, relative amount of litter (complete leaf litter, partial leaf litter, or bare soil), the amount of ground isolated by direct sunlight (estimated in 10% increments), and the highest and lowest substrate temperatures along with corresponding air temperatures 1.5 cm above the substrate. The extremes of air and substrate temperatures immediately accessible to each lizard were recorded to compare the range of environmental temperatures for each species and to correlate such temperatures with body temperatures. The substrate and air temperatures were recorded to the nearest 0.5°C with a YSI model 43TD telethermometer with a small banjo-type probe.

The lizard was collected either by hand, cork blowgun, rubber band, or .22 caliber dust shot, at which time its rectal temperature was immediately recorded to the nearest 0.1°C with a Schulteis quick-recording thermometer. In order to minimize heat transfer to the lizard it was held by its head or tail while its temperature was being recorded. The animal was preserved for later sexing, measurement, and analysis of stomach contents. Items in the stomach were identified to family and measured with a vernier caliper to the nearest 1.0 mm. Only intact, undistorted, freshly ingested food items were measured.

**All individuals were segregated into three age categories: adults, larger than the smallest female with developing ova; newly hatched, still retaining the umbilical scar; and immatures, intermediate to adults and newly hatched. These age categories were sufficiently distinct in size that they could be identified in the field.**

**RESULTS**

**Vegetation cover**

The relative height and arrangement of vegetation under which the lizards were observed is depicted in Figure 1 (d) as six specific locations (A through F) within a generalized diagram. A chi-square test of independence for foraging adults of each species, Figures 1(a), (b), and (c), resulted in a statistically significant difference in distribution among groups ($\chi^2 = 137.16$). Obviously, adult *A. quadrilineata* forage in areas distinct from foraging adult *A. leptophrys*. Statistically they are also distinct from foraging adult *A. festiva* ($\chi^2 = 49.44$). In addition, active adult *A. festiva* are distinct from active adult *A. leptophrys* ($\chi^2 = 9.49$), omitting location F where no individuals of both species were recorded, computed $\chi^2 = 22.68$). Usually *A. quadrilineata* was found foraging in the low vegetation adjacent to an exposed surface such as a road. It was never observed foraging on the forest floor. Similarly Hirth (1963) found that *A. quadrilineata* (on the east coast of Costa Rica) is "most abundant on the beach, and in the open, sunny area under coconut trees ..., but is never found in thick undergrowth." *Anomaca festiva* forages in the greatest concentration along the exposed forest edge (C in Fig. 1) but is also found inside the forest edge (B).

Since on several occasions adult *A. leptophrys* were observed basking before foraging, this behavior is noted in Figure 1(e). Intermittent basking during foraging is included with foraging in Figure 1(c). Foraging and basking are significantly different in distribution ($\chi^2 = 17.67$). This species appears to bask in the low vegetation at the forest edge, before moving to dense cover to forage. A comparison between Figure 1(f) and 1(b) shows that the distributions of newly hatched *A. leptophrys* and of *A. festiva* are not statistically dis-
tunguishable \( \chi^2_{0.05,14} = 9.49 \), omitting location F, computed \( \chi^2 = 2.73 \).

Vegetation cover directly or indirectly influences the degree of ground litter, the per cent of insolated substrate, and habitat temperatures. Although the following three sections treat these as separate entities, it is tacitly understood that they are interrelated.

Ground litter

Most of the lizards were observed on partial leaf litter (Fig. 2). The lowest per cent of any grouping was 65\% for adult foraging \( A. \) leptophrys. \( A. \) melita quadrilineata was the only species found on bare soil, while \( A. \) leptophrys (active adults) was the only species found in great numbers on complete leaf litter. Basking adults and active newly hatched \( A. \) leptophrys were found on similar ground litter composition as were active \( A. \) festiva adults.

Per cent of insolated substrate

Individuals were active only in direct or hazy sunlight and never during overcast conditions or rain. Foraging adults of \( A. \) quadrilineata were active on substrate with the highest per cent of insolation (74\%), compared with \( A. \) leptophrys (38\%), and \( A. \) festiva (60\%) (Fig. 3).

\[ \text{FIG. 3. Distribution of individuals (A.q. = A. quadrilineata, A.f. = A. festiva, and A.l. = A. leptophrys) with respect to per cent of ground insolated within a 3-m radius from the lizard.} \]

\[ \text{Fig. 4. Body temperatures of foraging individuals of all ages and environmental temperatures for the adults of each species and newly hatched \( A. \) leptophrys: S.H.—substrate hot, S.C.—substrate cold, A.H.—air hot, and A.C.—air cold. These environmental temperatures represent the highest and lowest substrate temperatures within a 3-m radius of the lizard along with corresponding air temperatures 1.5 cm above the substrate. The vertical line represents total range; the short horizontal line, arithmetic mean; and the rectangle, the 95\% confidence interval of the mean.} \]

\[ \text{A. leptophrys (} \bar{x} = 37.2^\circ \text{C). The range is defined as "preferred" body temperatures (Brattstrom 1965). These body temperatures parallel Bogert's (1949) observations of several species of} \text{Sceloporus which exhibited similar body temperatures even though they were widely separated ecologically. The recorded body temperatures are compared with the environmental temperatures of observed individuals (segregated to age). These environmental temperatures are found within the habitat corresponding to the locations in which the lizards were observed (Fig. 1). Although the body temperatures are not significantly different from each other, the environmental temperatures of \( A. \) quadrilineata are significantly greater than those of both \( A. \) festiva and \( A. \) leptophrys. In general, the environmental temperatures of \( A. \) festiva are greater than those of \( A. \) leptophrys, but only significantly so for air cold temperatures. Newly hatched \( A. \) leptophrys are active at environmental temperatures very similar to those recorded for \( A. \) festiva. Each species characteristically basks in an area exposed to direct sunlight, and after its optimum temperature is reached it forages for food either in shade or sunlight. It is assumed that while the lizard forages in the shade, its body temperature drops to its lower preferred limit, since the temperatures of the shade (i.e., air cold and substrate cold) all fall below the lowest recorded body temperature. To raise its body temperature again, the lizard seeks direct exposure to sunlight.} \]
TABLE 1. Comparison of adult snout-vent lengths for each species

<table>
<thead>
<tr>
<th>Species</th>
<th>Length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
</tr>
<tr>
<td>A. quadrilineata</td>
<td>69.9</td>
</tr>
<tr>
<td>A. festiva</td>
<td>102.2</td>
</tr>
<tr>
<td>A. leptophrys</td>
<td>119.5</td>
</tr>
</tbody>
</table>

Fig. 5. Rates of heat loss characteristic for each species. A single representative of each species and a newly hatched *A. leptophrys* were raised to 39°C and then tethered in the shade with air and substrate temperatures between 27°C and 29°C. The horizontal dot-dash line represents the average upper limit of the 95% confidence interval for the three species, while the horizontal dashed line represents the average lower limit of the range for the three species.

Rate of heat loss

The adults of each species differ significantly in size (Table 1) and it was assumed that the larger species, having smaller surface-volume ratios, would retain their body heat longer. The longer a lizard can retain its heat, the greater is its effective foraging area away from sunlight. This would be advantageous in forested areas of little sunlight.

In order to compare the normal rate of heat loss of the species to their thermal microclimate (Fig. 5), the body temperatures of an adult male of each species and a newly hatched *A. leptophrys* were raised to 39°C. The animals were then tethered in the shade (negligible wind) with air and substrate temperatures between 27°C and 29°C. These temperatures were chosen to correspond to the substrate cold and air cold temperatures noted in Figure 4. The larger *A. leptophrys* adult (83 g, 134 mm S-V) remained active about 2.6 times as long as the *A. quadrilineata* adult (10 g, 70 mm S-V), and about 1.9 times as long as the *A. festiva* adult (32 g, 102 mm S-V). The adult *A. leptophrys* retained its temperature above 35°C about six times as long as a newly hatched *A. leptophrys* (4 g, 55 mm S-V).

After the above experiment, the adults were tethered in the open sun to determine their critical thermal maximum (i.e., inability to right themselves when turned upside down, Brattstrom 1965) and their ability to thermoregulate according to modern theory (see discussion in Heath 1964). The critical thermal maximum of an *A. quadrilineata* was 42.8°C; of an *A. festiva*, 43.2°C; and of an *A. leptophrys*, 42.6°C. A differential of only 0.6°C for the three species suggests an overlap of critical thermal maximum to the same extent as body temperatures overlap.

Diurnal activity periods

During the study period, activity was recorded until there was an absence of observations over a period of an hour. Usually this corresponded to the event of rain in the afternoon, which greatly depressed foraging activity (1420 was the latest time any individual was observed). Since so few were observed after 1300, diurnal activity is noted only for the morning (Fig. 6). Although overlap occurs for all three species, their peaks of activity differ: *A. leptophrys* from 0900 to 0930, *A. quadrilineata* from 1100 to 1230, and *A. festiva* from 1030 to 1230. These results coincide with Hirth's (1963) results, in which *A. quadrilineata* was found to increase activity gradually until noon, and with Taylor's (1956) observation that *A. festiva* was "most active at about ten o'clock in the morning." Again basking and foraging are separated for adult *A. leptophrys*, in which it was found that the majority of individuals bask between 0800 and 0830. The peak foraging activity for newly hatched *A. leptophrys* occurred later in the morning, from 1130 to 1200, therefore differing from the adult's peak activity.

Selection of food items

From the stomachs that contained food items, 23 *Ameiva quadrilineata*, 21 *A. festiva*, and 14 *A. lepto-
phyris contained 129, 92, and 53 items, respectively. Of these food items a minimum of 63% for A. quadrilineata and a maximum of 83% for A. festiva were of the two orders Orthoptera and Araneida. (According to Milstead 1957, it has been found adequate to separate food items to the ordinal level.) Almost all of the items were arthropods except for two gastropods, one found in an A. quadrilineata and one in an A. leptocephrus, and two amphibians found in A. festiva. Even at the family level of separation in food items, considerable overlap between the three Ameiva was revealed, with, however, some notable exceptions. In particular, A. quadrilineata contained a higher per cent of Acrididae (62% of its items compared with 3.3% for A. festiva and 0.0% for A. leptocephus) and a lower per cent of Blattidae (4.7% of its items compared with 10.9% for A. festiva and 22.6% for A. leptocephus) than the other two Ameiva. Ants (Formicidae) and small spiders (Theridiidae) were eaten exclusively by A. quadrilineata and made up 12% of all items examined.

Stomach contents were also compared on the basis of food size. Figure 7 compares the per cent of individual food items, in 1.0 mm intervals, which were eaten by the adults of each species. Ameiva quadrilineata consumed significantly smaller items (x̄ = 9.3 mm) than either A. festiva (x̄ = 14.9 mm) or A. leptocephus (x̄ = 13.9 mm). The latter two species were not significantly different, with A. leptocephus eating slightly smaller items.

**Discussion**

Habitat selection with respect to vegetation cover is correlated with the amount of leaf litter and with the per cent of direct sunlight reaching the ground, which in turn influences the degree of substrate warming. The ground beneath low vegetation has a higher per cent of bare soil and direct sunlight than does the forest floor. Microclimatic temperatures are also higher in the low vegetation where A. quadrilineata occurs. Additional data and experiments are needed to identify the stimulus for the selection of a particular habitat, although it appears that sunlight and temperature are the most distinct features.

All three species maintain very similar body temperatures while foraging, but under different microclimatic temperatures and sunlight conditions. The preliminary experiment showing the rate of heat loss for each species was done in order to indicate what enables each species to maintain the same body temperature under different microclimatic conditions. Since the largest species, A. leptocephus (active in a habitat of greater shade), can maintain its body temperature at active levels longer than the other two species, the diameter of its effective foraging area away from sunlight is greater than that of A. festiva and especially that of A. quadrilineata. It follows that newly hatched A. leptocephus, capable of maintaining active temperature levels for only a short time, would be found in an area of greater sunlight and temperature. If it were in the same habitat as the adults on the forest floor, it could venture away from a sunny spot for only 2 min compared with the adult's 11 min, and would be limited to one-thirtieth the effective foraging area of the adult.

Active adult A. leptocephus have activity periods distinct from both active A. festiva and newly hatched A. leptocephus. Complete temporal separation does not occur, but there is definite separation between the peaks of adult A. leptocephus from A. festiva by 1.5 hr, and from newly hatched A. leptocephus by 2.5 hr. Cloudy weather may shift the activity peaks to later in the morning. Hirth (1963) has shown this to be true for A. quadrilineata.

Unfortunately, arthropods were not sampled in the specific habitats occupied by the three Ameiva to show if they actively select for type or size of food items available in their habitat. However, examination of stomach contents gives some cursory information on food habits, suggesting that differences in food type may be related to the occurrence of different species of arthropods in a specific habitat. For example, A. quadrilineata occupies an open area, which has a higher per cent of Acrididae (short-horned grasshoppers) and a lower per cent of Blattidae (cockroaches) than does the forest floor. Likewise, this is reflected in the items found in the stomachs.

The fact that the smallest Ameiva eat smaller items may also be a function of the habitat or it may be a function of body size, as Medica (1967) suggests for four sympatric species of Centrolenopus. That it is a function of body size is indirectly supported by Janzen and Schoener (1968), who found that small insects decrease in number moving from the forest to open areas of vegetation in Costa Rica. If this relationship is true in this study, then it follows that the smallest Ameiva species selects smaller arthropods in an area of predominantly larger arthropods. On the other hand, this positive correlation of body size to prey size is not supported by the fact that A. leptocephus eats slightly smaller items than the smaller A. festiva. However, this discrepancy may not be real. Janzen and Schoener (1968) found that less than 1% of 9,015 specimens of A. leptocephus may mean that neither A. festiva nor A. leptocephus can eat much larger items if the average length of items found in their stomachs is 15.2 mm; i.e., the upper 1% of arthropod size. Possibly all three species eat any palatable arthropod of the 'preferred' size available in its habitat, considering the indirect evidence for selecting size of item and the direct evidence (overlap of items eaten and the higher per cent of grasshoppers rather than cockroaches eaten by A. quadrilineata) for eating any type of arthropod available.

Interspecific competition reasonably may be assumed to be negligible (none was observed). However, it may have been an 'historical factor in the ecological differentiation' of these three coexisting Ameiva species. Coexistence is possible through establishment of effectively allopatric distributions even though they occur sympatrically in a given geographical area (Miller 1967). In this respect allopatry is demonstrated in this study at the level of feeding behavior; i.e., what they eat, where they eat, and when they eat. Each of these three aspects of feeding shows very little overlap between A. quadrilineata and A. leptocephus. However, A. festiva spatially overlaps these two species intermediate in location, but is
distinct since it eats at different times than *A. leptophrys* and eats larger food items than *A. quadrilineata*. Thus, ecological separation prevents interspecific encounters over a common food item and competition is avoided. As Schoener (1968) illustrates with sympatric species of *Anolis*, when overlap occurs in one segment of a niche, separation occurs in another portion of the niche.

Even though there is spatial overlap of basking *A. leptophrys* and foraging *A. fesitaca*, the two species effectively avoid competition since their peaks of activity are separated both temporally and behaviorally. Evidently, *A. leptophrys* basks on the outer edge of the forest clearing early in the morning to reach active foraging temperatures faster than if it remained in the well-shaded forest.

Newly hatched *A. leptophrys* overlap *A. fesitaca* with respect to vegetation cover, sunlight, microclimatic temperatures, ground litter, and activity periods. Possibly, since newly hatched *A. leptophrys* are smaller than adult *A. fesitaca*, active competition for food or possible basking sites will not occur, or if it does, the transitory age position of the newly hatched will not have long-term effects on the population dynamics with respect to reproductive adults.

In summary, these three sympatric species of lizards do show differences in their ecology. They are found under different degrees of vegetation cover (from dense to open), which in turn is correlated to the per cent of direct insolation of the ground, the amount of substrates warming, and the degree of leaf litter. The maintenance of similar body temperatures by all three species while foraging in different thermal environments may be partially a function of body size. Activity periods appear to be distinct, but with considerable overlap. Selection of food items may be a function of availability within the habitat for type of arthropod and a function of body size to size of item eaten.

**Literature Cited**


**SIZE OF BREEDING COLONY RELATED TO ATTRACTION OF MATES IN A TROPICAL PASSERINE BIRD**

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*Abstract.* Field observations and counts of nests and birds present were made for 18 colonies of the Village Weaverbird, *Ploceus (Textor) cucullatus*, in north-west Senegal during the breeding season of 1967. In this gregarious and polygynous species, the male weaves the nest and then endeavors to attract the female to the nest by means of special displays and vocalizations. Breeding colonies with fewer than 10 males had a much smaller proportion of females resident in the colony at or near the peak of colony growth than did larger colonies (chi-square test, *P* = .018).

The species is near the northern border of its range near the Sahara in this region and presence or absence of sufficiently large trees is at times a crucial factor limiting local distribution of colonies. Although large trees in general tend to have larger colonies than do small trees, success of a colony in attracting females was correlated much more with number of males and nests than with size of tree. It is concluded that the evolution of gregarious breeding in this species was in part due to the increased efficiency of attracting mates that results from colony life.

This report deals with a field study made in West Africa of the Village Weaverbird, *Ploceus (Textor) cucullatus cucullatus* (Müller), during its breeding season in 1967. The objectives of this study were to investigate some aspects of social organization in relation to colony size and to local distribution of breeding populations in a highly sociable land bird. There seems to be no previous study that has focused attention on the possible relationship between size of colony and attraction of mates to the colony. A further objective was to at-