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Differences in habitat use of two sympatric species of *Ameiva* in East Costa Rica

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Abstract. Identifying the differences in habitat use for sympatric species is important for understanding the species preferences and the limits of population distribution. We studied the differences in the habitat use of two understudied sympatric species of *Ameiva* (*A. festiva* and *A. quadrilineata*) in a natural reserve of the Caribbean coast of Coast Rica. *Ameiva quadrilineata* showed a more restrictive habitat use pattern than *A. festiva*. *A. quadrilineata*'s smaller body size may be one of the factors limiting its habitat range. Both species showed higher density in regenerated forests, while *A. quadrilineata* was never found in swamp forests. The air temperature and the meteorological condition at the moment of the survey also influenced the occurrence of the *A. quadrilineata*, while the juveniles of *A. festiva* were only affected by the meteorological condition. None of the studied variables seemed to affect the occurrence of *A. festiva* adults. The results of this study can be useful to evaluate possible changes in the species distribution patterns as a consequence of direct (i.e., deforestation) or indirect (i.e., climate change) human activities in the distribution area of these species.

Keywords. Habitat use, activity pattern, GLMMs, Costa Rica, *Ameiva*.

Understanding which factors influence habitat use patterns may be of major importance to evaluate the threatened status of the species and to develop management strategies. It is especially urgent nowadays because of the difficulty of separating human impacts from natural stochastic events (Pechmann et al., 1991). Environmental conditions may change due to human-induced global climate change (Sinervo et al., 2010) and there is a need to identify the species' habitat requirements to develop management strategies accordingly. Moreover, the patterns of habitat use in reptiles are very linked to the species-specific thermal restrictions. Lizard species may differ in their ability to use habitats with different solar exposure by having different morphology, physiology or behaviour (Pianka and Vitt, 2003). For example, lizards foraging in shaded areas rapidly cool as a consequence of low thermal inertia and they need to newly expose directly to the sun to

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raise their body temperature. Consequently, it is important to combine data on patterns of habitat use with the thermal information to develop more accurate management strategies for reptiles.

In tropical areas there is a lack of scientific information about the basic ecology of many species (Peres, 2005). The lack of funding, or the difficulties in the accessibility to the natural areas are some of the causes of this information deficiency (Sodhi, 2008). In the tropical Pacuare Reserve (Caribbean coast of Costa Rica, 10°13'N, 83°15'W; maximum altitude of 1 m a.s.l.) two species of lizards from the genus *Ameiva* (*A. festiva* and *A. quadrilineata*, Teiidae) have been identified (Abella et al., 2008). The populations of these two species overlap in their distribution, but previous studies have identified differences in their specific habitat (Hillman, 1969). The information related to these two species is dated and not abundant, referring basically to their temperature preferences (Hirth, 1964), ecology (Hirth, 1963; Hilman 1969; Vitt and Zani, 1996) and reproduction (Smith, 1968). Specifically, Hillman (1969) found that *A. quadrilineata* occurred with a higher frequency (74% of occurrence) at low vegetation with a high percent of insolated substrate, while *A. festiva* was found foraging both in the edge and inside the forest and with a lower insolation (60% of occurrence). However, the available information on their occurrence in different habitat types still has many gaps.

We know from previous studies that, for species with similar thermal preferences and tolerance limits, larger lizards will loss heat with a slower rate than the smaller ones, permitting longer times without a direct exposure to sun (Asplund, 1974; Stevenson, 1985). We also know that *A. quadrilineata* is slightly smaller than *A. festiva*, so its ability to stay away from sunny areas might be smaller, but their thermal preferences and tolerance limits are similar (Hillman, 1969). Thus, the aims of this study are: (i) to evaluate the habitat use and activity patterns of two sympatric species of *Ameiva*; (ii) to qualitatively assess if the possible differences in habitat use agree with the differences in thermal inertia between the two species due to changes in body size. We hypothesized that the habitat requirements of *A. quadrilineata* may be more limited than those of *A. festiva*.

We randomly selected eight transects (100 m length) following the approach outlined by Heyer et al. (1994). We selected two transects by each of the four main habitat types. The "Sandy forest" is formed by all the vegetation related to the sandy beach, including several plants adapted to the high salinity and the marine influence. All plants are relatively small (not taller than 3 m) and the soil is formed by volcanic grey sand. The "Regenerated forest" includes re-grown forests in old open pasture previously used for cattle ranching, and abandoned since 1989. It is composed by many species of medium-small trees (diameter less than 30 cm), such as *Zygia longifolia*, or *Prioria copaifera*. The forest composition of the "Secondary forest" is similar to the one in the "Regenerated forest", but the trees are older (the diameter can be more than 30 cm for some trees) and the forest is more mature. The trees and shrubs density is higher and there is, in general, less light reaching the soil. Finally, the "Swamp forest" is located close to a small pond with permanent water, and soils surrounding the pond retain water for long periods of time each year. The vegetation is dense, dominated by *Raphia taedigera* and there are other species such as *Zygia longifolia,* and *Erythrina cochleata*. The area floods easily when the rain is strong.

The surveys were performed at three different times of the day: in the morning (5:30-7:30), midday (12:00-14:00) and evening (16:00-18:00), but the same transect was only surveyed once a day. The meteorological condition (sunny, partially cloudy, cloudy, raining), the air temperature (in Celsius degrees), the relative humidity, and the precipitation (raining, last rain less than one hour ago, between one and five hours ago, between five and ten hours ago, between ten and 24 and more than 24 h ago) were identified. We used a digital thermometer (precision ± 1 °C) for measuring the temperature and a hygrometer (precision ± 1%) for relative humidity. Each transect was walked slowly, fitting the total survey time to 15 minutes. The number of times each transect was walked varied between 12 and 22 times (average 16.2 times). The occurrence of individuals of *A. festiva* and *A. quadrilineata* was recorded, distinguishing between adults and juveniles. We distinguished juveniles and adults depending on the body size. Juveniles of *A. festiva* were shorter than 7.8 cm while juveniles *for A. quadrilineata* were shorter than 6.2 cm (Savage, 2002). We could not effectively identify males from females and therefore sexual differences were not analysed. At the detection points we measured some microhabitat variables: the total height from the soil layer; the litter height; the distance between the soil and the location of the individual at the dead leaves. We also measured the exposure degree of the individual to the sun (shade, filtered sun or sun), the air temperature, and the relative humidity.

Generalized linear mixed models (GLMMs) with the R 2.1.1 software (R Development Core Team, http://www.r-project.org) were used to relate the abundance of both species in each transect to environmental and habitat variables. We calculated the abundance as the numbers of *Ameiva* individuals of each species per transect, and it was used as the dependent variable for the models. Because the activity and abundance of the species can change depending on the time of the day, we included this variable as a covariate. Moreover, as we surveyed the same transects several times, we also included transect as a random variable. We constructed one multivariate model to assess the effect of the environmental variables, and one univariate model to evaluate the habitat preferences. We built four separate models to evaluate the differences between species and ages: one model for adults and one for juveniles for each of the two species. GLMMs permit the use of suitable error distributions, and some of the limitations of conventional regression models were avoided. We used the Poisson distribution as error function and the glmer function from the lme4 package. For the multivariate model, we used a backward removal procedure to obtain a final model containing only significant factors that significantly improved the fit of the model by more than 1% of the explained deviance (see Santoul et al., 2004 for a similar approach). Finally, we used non-parametric tests to analyse the differences between the species and between adults and juveniles at the microhabitat level.

We observed a total of 190 individuals. From these individuals, 155 were *A. quadrilineata* (70 adults and 85 juveniles), and 35 were *A. festiva* (17 adults and 18 juveniles) in 132 transects (36 in regeneration forest, 39 in secondary forests, 26 in swamp forests and 32 in sandy areas).

The final models explaining the environmental factors affecting abundance along transects were similar for both species (Table 1). Juveniles of *A. festiva* were affected by the meteorological condition, while juveniles of *A. quadrilineata* were also affected by the temperature. Only the adults of A. *quadrilineata* were significantly affected by the temperature. Moreover, the best time of the day for surveying was at midday for both species (Fig. 1). Previous studies have associated the activity of *A. festiva* with the time of day

Table 1. Summary of the results from the two final set of GLMMs for the two species and for each of the two considered stage (adult, juvenile). Model 1 stays for GLMM built using environmental variables as predictors; in model 2 the only predictor is the habitat type. Time of the day was included as a covariate while survey was included as a random variable. Coefficients (Coeff) and associated P-values (P) are shown for the variables included in the final models. Temp: air temperature; MC: meteorological condition.

Species	Model	Stage	Variable	Coeff.	P
A quadrilineata	1	Adult	Temp	0.569	<0.001
		Juvenile	Temp	0.521	<0.001
			MC	0.645	0.035
A. festiva	1	Adult	Temp	0.209	0.013
		Juvenile	MC	-0.976	0.028
A. quadrilineata	2	Adult	Habitat	-1.197	0.006
		Juvenile	Habitat	-0.244	0.244
A. festiva	2	Adult	Habitat	-0.297	0.192
		Juvenile	Habitat	-0.253	0.658

when temperatures and sun exposure are maximum, both of which appear necessary for attainment of high activity body temperatures (Vitt and Zani, 1996).

The insolation and the precipitation did not affect the occurrence of any of the species. Hirth (1963) affirmed that the activity of Teiidae almost comes to a stop when clouds hide the sun. *Ameiva* individuals were found with a higher frequency in sunny days in the study area. Nevertheless, they were also observed active in partially cloudy, and even in cloudy days. *A. festiva* had already been observed in these meteorological conditions (Vitt and Zani, 1996), but no records had been found before for *A. quadrilineata* (Hirth, 1963; Hillman, 1969).

The habitat use patterns differed between *A. festiva* and *A. quadrilineata*, and also between adults and juveniles. *A. quadrilineata* was distributed differentially in the four habitats, while *A. festiva* did not show any pattern (Table 1 and Fig. 2). When lizards forage in the shade, their body temperatures drop to their lower limit, since the temperatures of the shade (i.e., air cold and substrate cold) normally falls below the lowest recorded

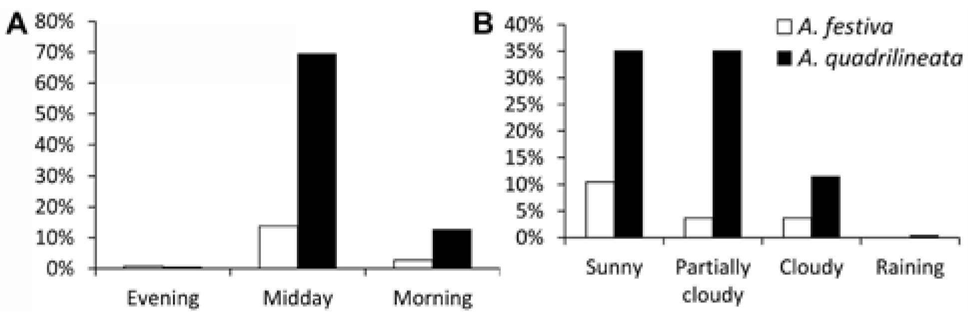

Fig. 1. Histograms comparing the percentage of the observations at each time of the day (A) and for each meteorological condition (B) for both studied species.

body temperature (Huey and Tewksbury, 2009). To raise their body temperature again, the lizards may seek direct exposure to sunlight. As the body size of *A. quadrilineata* is small, its cooling rate may be higher than the one of *A. festiva* (it needs about three more minutes than *A. quadrilineata* for its body temperature to decrease six degrees; Hillman, 1969), and this may be influencing the differences in habitat use found for the two species. Vegetation cover also directly or indirectly influences substrate and habitat temperatures. This agrees with the finding that the occurrence of *A. quadrilineata* in dense vegetated areas was less frequent and it was never found in habitats without areas with direct sun exposure (Hirth, 1963; Hillman, 1969).

Ameiva festiva showed a different pattern occurring in all habitat types without presenting significant habitat preferences. The larger body size of this species allowed it to stay longer periods of time away from the direct exposure to the sun (Hillman, 1969; Vitt and Zani, 1996), and it was often detected both in secondary and swamp forests. Its ability to shuttle between sun and shade helps this species to maintain the body temperature at high constant level (see van Berkum, 1986 for a similar behaviour in *Anolis* species). It is important to notice than other variables, such as differences in the behaviour and differences in their physiology may also be influencing their dissimilar ability to use the studied habitat types and further studies are required in order to confirm our hypotheses.

Ameiva juveniles did not show strong differences in habitat use with respect to adults (Fig. 2). Even, the density of *A. quadrilineata* juveniles at the sandy forest (the area with the highest insolation degree) was higher than for the adults. Moreover, juveniles of *A. festiva* presented high densities in swamp and regeneration forests. The small number of observations for *A. festiva* can bias the results for this species.

At the microhabitat level, significant differences between species emerged in the temperature (Mann-Whitney U-test, U = 2064, P = 0.027) and relative humidity (U = 3453, P = 0.012) when both species were found. As *A. quadrilineata* is smaller, it is more affected by changes in environmental temperature and insolation (Hillman, 1969) and its activity is related to a combination of adequate temperatures with other environmental variables such as the meteorological condition (i.e., sunny days). The observed temperature ranges for *A. festiva* were broader than those observed in previous studies in a population in

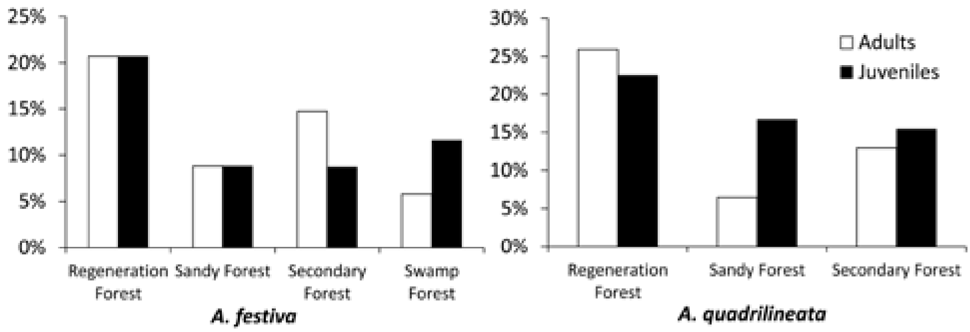

Fig. 2. Histogram representing the percentage of observations found at the four habitat types for adults and juveniles of the two studied species.

Southeastern Nicaragua (between 27-37 in our study and 26-32 in Vitt and Zani, 1996). *Ameiva festiva* was found at higher relative humidity than *A. quadrilineata* (peak of 82% vs. 68%). This can be related to differences in skin water loss between species, but experimental studies are required to confirm the existence of these differences. We did not find differences in the soil and death litter height where the individuals of the two species were found. Moreover, we also compared the temperature and relative humidity between adults and juveniles. We found differences for *A. quadrilineata* (Mann-Whitney U-test: temperature, $U = 2354$, $P = 0.026$; relative humidity, $U = 3693$, $P = 0.010$), but not for *A. festiva*. The temperature of *A. quadrilineata* varied from 34.2 to 33.4 °C (adults-juveniles) and the relative humidity from 69.3% to 72.5%.

To sum up, we have shown differences in the habitat selection and in environmental variables determining the occurrence of *A. festiva* and *A. quadrilineata* in our study-area. These results can be useful to evaluate possible changes in the species distribution patterns as a consequence of direct or indirect human activities in the distribution area of these species. Because lizards have in general very strict thermal requirements, climate change is one of the most important human activities that can affect *Ameivas'* distribution (Huey et al., 2009). If the temperature in an area changes, the species will move to other areas, adjust to the new environment, or get extinct (Sinervo et al., 2010). Moreover, climate change can also benefit some reptile species if the area with the preferred temperature is increased. Anyway, a more detailed knowledge on the habitat and thermal preferences of the species can be used to model possible changes in the distribution and in the behaviour of the focal species, and the consequences of global warming on the population.

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