
Ameiva fuscata on Dominica, Lesser Antilles: natural history and interactions with *Anolis oculatus*

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ABSTRACT — In June 2008, we studied the natural history of *Ameiva fuscata* and interactions with sympatric *Anolis oculatus* in five adjacent habitats on the western (leeward) coast of Dominica, Lesser Antilles. *Ameiva* activity was positively correlated with mean temperature, peak activity corresponded to peak daily temperatures and we observed greatly reduced or no activity during overcast and rainy periods. Population densities in the five habitats were 138–344 lizards/ha, with the higher densities in areas with the deepest leaf litter and densest canopy cover. *Ameiva fuscata* is an active forager, with 100% of foraging attempts made while moving (either walking or actively digging or rooting in litter). Lizards foraged together in groups and the groups never entered each other's activity areas, suggesting the possibility of community structure. *Ameiva fuscata* is non-territorial, but chases among adult males appeared to be triggered by intersecting paths. Anoles spent significantly less time on the ground when *Ameiva fuscata* was active, presumably to avoid predation.

WEST Indian islands support abundant and diverse lizard communities. Common elements of many of these communities include an active foraging terrestrial lizard in the genus *Ameiva* and arboreal sit-and-wait ambush foragers in the genus *Anolis* (Simmons et al., 2005). Although West Indian anoline lizards are arguably the most intensely studied reptiles in the world (Losos, 2009), relatively little is known about most species of West Indian *Ameiva*, especially considering their visibility on the islands where they occur (Henderson & Powell, 2009).

Ameiva are typically heliothermic, active foragers, have relatively short activity periods, are not territorial and have overlapping home ranges (e.g., Hillman, 1969; Regal, 1978, 1983; Schell et al., 1993; Vitt & Colli, 1994; Simmons et al., 2005). *Ameiva fuscata* (Fig. 1; and front cover) is endemic to Dominica and occurs throughout the island in coastal woodlands, generally at elevations below 200 m, but occasionally higher in cultivated areas (Bullock & Evans, 1990; Malhotra & Thorpe, 1999).

Despite the number of islands on which both genera are represented, few studies have addressed

interactions between *Ameiva* and *Anolis*. Meier & Noble (1991, Desecheo), Fobes et al. (1992, Hispaniola) and Eaton et al. (2002, Anguilla) suggested that anoles decrease time spent on the ground in the presence of *Ameiva*. Simmons et al. (2005) examined interactions between *Ameiva ameiva* and two species of *Anolis* (*A. aeneus* and *A. richardii*) on Grenada and concluded that both species of *Anolis* spend less time on the ground when *A. ameiva* is active. Kolbe et al. (2008) showed a niche shift by *Anolis watsi* to lower perches and more terrestrial activity in the absence of *Ameiva griswoldi* on Antigua satellite islands.

From 4–23 June 2008, we conducted a study on Dominica to describe activity, population densities, foraging behaviour and movements of *Ameiva fuscata* and to test the hypothesis that *Anolis oculatus* (Fig. 2) would spend less time on the ground when *A. fuscata* is present and active.

METHODS AND MATERIALS

Our study site was at the mouth of the Batali River on the leeward (western) coast of Dominica (N 15° 27.12', W 061° 26.76'). The site was characterised by habitats including beach,

| Area | Size (m ²) | Insolation | Most Abundant Vegetation | Maximum Number | Estimated Density (#/ha) |
|------|------------------------|-------------|--------------------------|----------------|--------------------------|
| 1 | 1134 | mixed | ground scrub | 39 | 344 |
| 2 | 2035 | sunny/mixed | Snake Plant | 28 | 138 |
| 3 | 2554 | mixed | Mango trees | 62 | 243 |
| 4 | 873 | shade/mixed | scrub, trees | 15 | 172 |
| 5 | 1925 | shade/mixed | Coconut trees | 57 | 296 |

Table 1. Characterisation of areas/habitats (see text) and maximum numbers of *Ameiva fuscata* observed during any one survey.

beachside scrub with Sea Grape (*Coccoloba uvifera*) and dry forest interspersed with Mango trees (*Mangifera* sp.). Cleared paths passed between and extended into most areas. Open areas were characterised by grasses, herbaceous forbs and stands of ornamental vegetation, including extensive areas planted in “Snake Plant” (*Sanseveria* sp.).

The five habitat areas (Table 1) were identified after observing what appeared to be natural groupings of *Ameiva* associated with areas of high population densities and corresponding roughly to distinct habitat types. Areas/habitats were characterised by: (1) mix of native and orchard trees with a canopy coverage of 50–80% and a sparse 2–3 m high understory, canopy height of 5–15 m with litter depth of 2–4 cm and occasional human traffic; (2) beachside vegetation with 1–2 m-high understory, canopy coverage of 20–50%, canopy height 4–12 m, sandy substrate with some leaf litter and regular human traffic; (3) orchard trees with sparse 2–4 m-high understory in some areas, canopy coverage ca. 90% over part of the area and ca. 10% over the remainder, canopy height 5–20 m with litter depth of 1–2 cm, abundant fallen fruit and occasional human traffic; (4) mix of native and orchard trees with canopy coverage of 60–90% and a dense 1–2 m-high understory, canopy height of 5–20 m with a litter depth of 1–2 cm and occasional human traffic; and (5) orchard trees with canopy coverage of 70–90%, leaf litter depth 2–4 cm, abundant fallen fruit, sparse understory and little human traffic.

We conducted 17 45-min surveys at various times from 0700–1730 h, recording time, extent of cloud cover and any precipitation during each visit. Systematically covering each area in a

manner designed to avoid multiple encounters with the same lizards, we counted the number of individual *Ameiva fuscata* observed in each of the five contiguous habitats and calculated estimated population densities (numbers of animals/ha) using the maximum number of lizards in any one area at one time relative to the areas (m²) sampled. A data logger (HOBO® TidbiT® v2 Submersible Temperature Logger, Onset Computer Corp., Bourne, Massachusetts, USA) was placed in leaf litter at site 5 to record hourly temperatures during the extent of the study.

We conducted focal animal studies on *A. fuscata*. Observations ranged from < 1 min to 20 mins in duration. In addition to recording anecdotal observations of individuals or groups of lizards, we quantified behaviours using methods of Cooper et al. (2001), recording time spent moving, number of moves and number of feeding attempts while stationary or mobile. We used these observations to calculate moves per minute (MPM), percent time spent moving (PTM) and proportion of feeding attempts while moving (PAM).

Using a paint gun (Forestry Suppliers, Inc., Jackson, Mississippi, USA) and two colours of latex paint diluted 1:1 with water, we marked individual *A. fuscata* active in areas 2 and 5 (along the beach and in a densely shaded area among large boulders), attempting to paint all individuals in three sessions at each location. The two sites were only ca. 40 m apart and no evident barriers precluded movement between the areas. We then observed movements and behaviours of marked lizards to determine if lizards foraging in one area comprised a grouping distinct from those in the other.

In the same five adjacent habitats, at various times of day and under varying weather conditions, we



Figure 1. Adult male *Ameiva fuscata*. Photograph by Robert Powell.



Figure 2. Adult male *Anolis oculatus*. Photograph by Robert Powell.

conducted 43 10-min surveys of anoles, recording lizard position as either on the ground or on elevated perches (e.g. vegetation or rocks). Anoles were not marked and we may have encountered the same individuals more than once. However, we contend that perches at different times and on different days are independent events predicated by either the presence or absence of *Ameiva* and that we are not guilty of pseudoreplication of data. We recorded time, temperature and general weather conditions during each survey and noted whether *A. fuscata* was abundant and active (1), scarce (2), or absent (3).

Temperatures were highest just as activity began to decline. The maximum observed population density in any one area was 344 individuals/ha (Table 1). That with the highest density had the deepest leaf litter and the densest canopy cover. Mean MPM for all *A. fuscata* was 2.1 ± 0.2 (0.2–4.9). Mean PTM was $43.8 \pm 3.3\%$ (3.0–98.2%). PAM was 100%, with 55.6% of feeding attempts occurring while animals were searching and 44.3% while in one location but actively digging.

Painted individuals were observed daily. The two “subpopulations” were never observed to

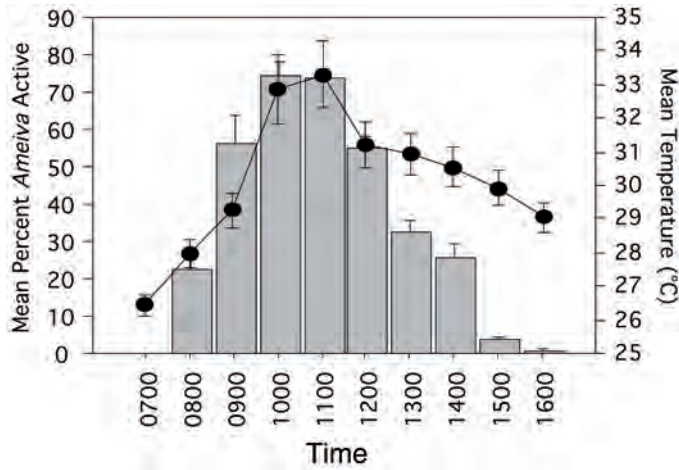


Figure 3. Mean percent of *Ameiva fuscata* active in all areas and mean ambient surface temperatures by time of day.

We used StatView 5.0 (SAS Institute, Cary, North Carolina, USA) for statistical analyses. Means are presented \pm one SE. For all tests, $\alpha = 0.05$.

RESULTS

Ameiva activity (percent of the maximum number of *Ameiva* observed in a given area) was positively correlated with mean temperature (Spearman Rank Correlation, $Z = 2.46$, $P = 0.01$; Fig. 3), showing clearly that a single peak activity period corresponded with peak daily temperatures. We observed greatly reduced or no activity during overcast and rainy periods, even at times when *Ameiva* were usually active. Observed activity periods were from 08:00–16:00 at a mean surface temperature of $30.1 \pm 0.7^\circ\text{C}$ (26.4–33.3°C), with a peak during late morning (09:30–11:30).

co-mingle and never found in areas other than where they were initially painted.

We frequently observed individuals of all sizes foraging together with few interactions between lizards. However, large males regularly chased one another. These chases would sometimes occur between individuals that had been foraging close together for several minutes. In most instances, no obvious cause could be discerned. However, based on five observations, the angle at which paths of moving individuals intersected appeared to trigger at least some chases (i.e., when a large male was about to intersect the path of another large male).

We observed 618 anoles during 43 10-min surveys (289 on the ground, 329 on elevated perches). The mean percent of anoles observed on the ground during all survey periods was $44.7 \pm 4.4\%$ (Fig. 4), but this percent varied considerably

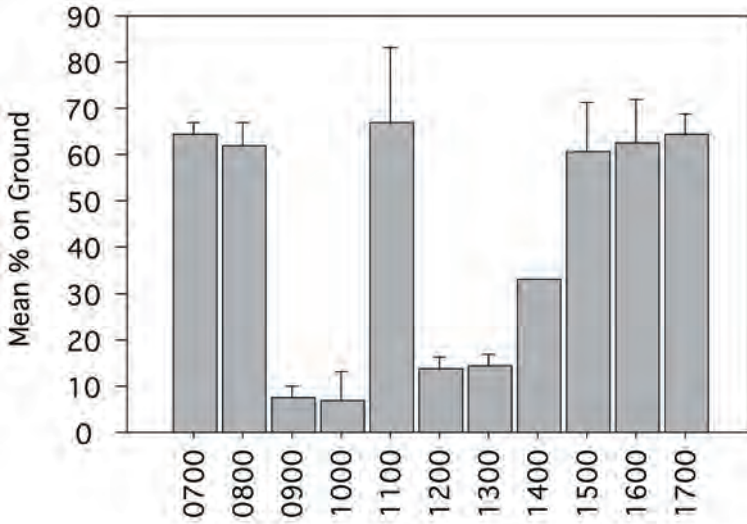


Figure 4. Mean percent of *Anolis oculatus* observed on the ground throughout the day.

throughout the day (Fig. 5). Significantly fewer anoles ($12.2 \pm 1.7\%$) ventured onto the ground when *Ameiva fuscata* was abundant and active than when few individuals were active ($21.9 \pm 6.7\%$) or when no *Ameiva* ($66.9 \pm 2.5\%$) were seen (one-way contingency tests, all $\chi^2 \geq 150.4$, all $P \leq 0.0001$). Anoles were found on the ground in high numbers at times of day when *Ameiva* were not active (07:00–08:00 and 15:00–17:00), but also during rainy/overcast periods, even at times when

A. fuscata usually is active (the large number on ground at 11:00 in Fig. 4 reflects observations on rainy days).

DISCUSSION

Previous studies conducted at the same time of year have shown that some populations of *Ameiva* (*A. chrysoleama*, Schell et al., 1993; *A. ameiva*, Simmons et al., 2005) exhibit two activity peaks, but that was not evident in this population of *A.*

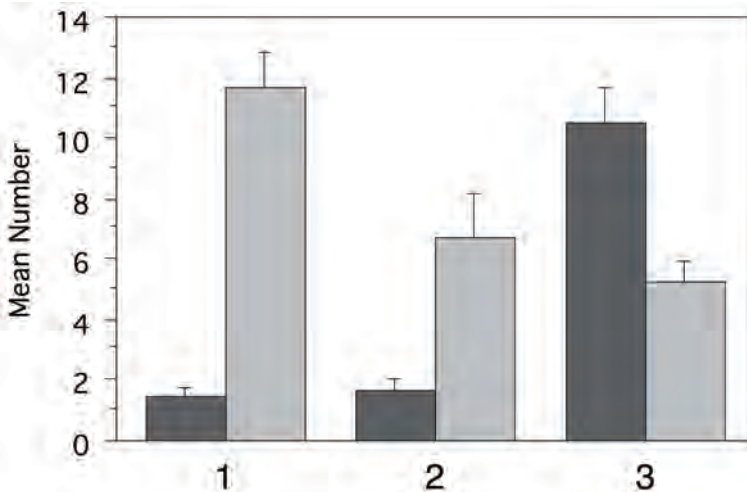


Figure 5. Mean number of *Anolis oculatus* observed on the ground (dark grey) and on elevated perches (light grey) per 10-min survey at different levels of *Ameiva fuscata* activity (abundant and active = 1, scarce = 2, or absent = 3).

fuscata. Observed activity periods and the maximum observed population density corresponded with activity periods and the maximum density (379/ha) observed by Bullock & Evans (1990) for *A. fuscata*. Although our estimates of density are undoubtedly conservative (as they are based on the maximum number of lizards seen at only one time), they are higher than most other population density estimates for West Indian species of *Ameiva*. Meier et al. (1993) calculated 73.7–81.1 *A. polops*/ha on Green Cay (U.S. Virgin Islands); Schell et al. (1993) presented an estimate of 136–144 *A. chrysolaelma*/ha in an altered habitat in the Dominican Republic; Censky (1996) found 74 *A. pleii*/ha on Anguilla and 91/ha on Dog Island; McNair (2003) presented crude and ecological densities of 25 and 128 *A. polops*/ha, respectively, on Protestant Cay (U.S. Virgin Islands); and R. Powell & R.W. Henderson (unpubl. data) estimated 33.8–52.2 *A. exsull*/ha on Guana Island (British Virgin Islands). Only Simmons et al. (2005) calculated a higher density, 460 adult *A. ameiva*/ha in an “activity area” on Grenada. Because population sizes were estimated using different methods, however, direct comparisons may not be appropriate.

Maximum observed densities of *A. fuscata* presumably reflect the availability of resources in each area. Those with the highest density (Table 1) had the deepest leaf litter and the densest canopy cover. Abundant leaf litter may harbour more abundant prey. The high tolerance of shaded habitats is unusual in West Indian species of *Ameiva*, which generally are associated with open situations (Henderson & Powell, 2009). Historically, however, open habitats may have been present on Dominica only intermittently after hurricanes, forcing the species to adapt to areas with closed canopies, in which they exploit small sun-lit patches to bask.

Observed values for MPM, PTM and PAM are comparable to those observed by Simmons et al. (2005) for *A. ameiva* (MPM = 5.6 ± 0.5 , PTM = $51.2 \pm 3.9\%$, PAM = $96.0 \pm 2.0\%$). Cooper et al. (2001) described PAM as a means of quantifying foraging methods in conjunction with MPM and PTM. Our data clearly indicated that *A. fuscata* employed an active foraging strategy, which is characteristic of teiid lizards in general (Cooper et al., 2001) and West Indian species of *Ameiva* in

particular (e.g., Hodge et al., 2003).

Home ranges of West Indian species of *Ameiva* are known to overlap (e.g., Kerr et al., 2005; Simmons et al., 2005) and appear to vary considerably in size. Simmons et al. (2005) recorded mean home range sizes for *A. ameiva* on Grenada of 648 ± 252 m² (adult males) and 204 ± 55 m² (adult females). Censky (1995) noted larger home ranges for *A. pleii* on Anguilla (1551 ± 566 m² for males, 864 ± 504 m² for females). However, those observed by Lewis & Saliva (1987) for *A. exsul* on Puerto Rico (377 m², 174 m²) were slightly smaller and those reported by Schell et al. (1993) for *A. chrysolaelma* in a partially confined habitat in the Dominican Republic (250 ± 122 m², 115 ± 102 m²), by Meier et al. (1993) for *A. polops* on Green Cay off St. Croix (190 ± 86 m² for both sexes) and by Kerr et al. (2005) for *A. erythrocephala* on St. Eustatius (101 ± 36 m², 54 ± 12 m²) were considerably smaller. The consistency with which marked *A. fuscata* were resighted only in those areas where originally seen during the current study suggests that groups of individuals have relatively small home ranges where population densities are high. That individuals with the same paint colour were consistently observed together also was suggestive of a previously undescribed community structure. In addition, individuals were frequently observed making foreleg movements that appeared to serve a communicative function and seemed to be directed at other lizards within the group. Furthermore, individuals often interrupted foraging behaviour and appeared to monitor the activity of nearby animals.

Ameiva fuscata and congeners in general have been described as non-territorial (e.g. Schell et al., 1993; Hodge et al., 2003) and observations of individuals of all sizes foraging together supported that contention. However, large males occasionally chased each other while foraging, which would indicate that defence of individual space may occur. This aggression appears to be triggered by the angle at which paths of actively foraging individuals intersect. Mate-guarding, which has been described for some populations of *A. pleii* (Censky, 1995), also might result in agonistic interactions, but we observed only one instance of what might have been construed as mate-guarding.

At our study site, *Anolis oculatus* was active from dawn to dusk (N.J. Vélez Espinet & E.A. Daniells, unpubl. data). Time spent on the ground by anoles was not dependent on the time of day or any single environmental condition, but instead appeared to be influenced primarily by the presence of *Ameiva*. As proposed by Simmons et al. (2005) and supported by our observations of successful predation on anoles by *Ameiva*, the principal cause of this behaviour by anoles appears to be predator avoidance.

In general, our observations suggest that the natural history of Dominican *Ameiva fuscata* is generally comparable to that of other West Indian congeners. These lizards are largely terrestrial, heat-loving, non-territorial active foragers. At our study site, however, they did not exhibit the bimodal activity period evident in at least some populations of some congeners and their predilection for foraging in heavily shaded areas was unusual. Observations of possible community structure and that aggression between adult males might be triggered by intersecting trajectories of moving lizards are new. Although these phenomena currently are supported solely by anecdotal data, they are worthy of further investigation. Also, despite warnings by Micco et al. (1997) that information pertaining to a single population might not be extrapolated accurately to other populations (much less to other species), responses by *Anolis oculatus* to *Ameiva fuscata* were essentially similar to those observed between anoles and *Ameiva ameiva* on the island of Grenada (Simmons et al., 2005).

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REFERENCES

- Bullock, D.J. & Evans, P.G.H. (1990). The distribution, density and biomass of terrestrial reptiles in Dominica, West Indies. *J. Zool. (Lond.)* **222**, 421–443.
- Censky, E.J. (1995). Mating strategy and reproductive success in the teiid lizard, *Ameiva plei*. *Behavior* **132**, 529–557.
- Censky, E.J. (1996). The evolution of sexual size dimorphism in the teiid lizard *Ameiva plei*: A test of alternative hypotheses. In: *Contributions to West Indian Herpetology: A Tribute to Albert Schwartz*, pp. 277–289. Powell, R. & Henderson, R.W. (Eds.), *Contributions to Herpetology*, Vol. 12. Ithaca, New York: Society for the Study of Amphibians and Reptiles.
- Cooper, W.E., Jr., Vitt, L.J., Caldwell, J.P., & Fox, S.F. (2001). Foraging modes of some American lizards: Relationships among measurement variables and discreteness of modes. *Herpetologica* **57**, 65–76.
- Eaton, J.M., Larimer, S.C., Howard, K.G., Powell, R., & Parmerlee, J.S., Jr. (2002). Population densities and ecological release of a solitary species: *Anolis gingivinus* on Anguilla, West Indies. *Carib. J. Sci.* **38**, 27–36.
- Fobes, T.M., Powell, R., Parmerlee, J.S., Jr., Lathrop, A., & Smith, D.D. (1992). Natural history of *Anolis cybotes* (Sauria: Polychridae) in a disturbed habitat in Barahona, Dominican Republic. *Carib. J. Sci.* **28**, 200–207.
- Henderson, R.W. & Powell, R. (2009). *Natural History of West Indian Reptiles and Amphibians*. Gainesville, Univ. Press of Florida.
- Hillman, P.E. (1969). Habitat specificity in three sympatric species of *Ameiva* (Reptilia; Teiidae). *Ecology* **50**, 476–481.
- Hodge, K.V.D., Censky, E.J., & Powell, R. (2003). *The Reptiles and Amphibians of Anguilla, British West Indies*. The Valley, Anguilla National Trust. 72 pp.
- Kerr, A.M., Powell, R., & Parmerlee, J.S. Jr. (2005). *Ameiva erythrocephala* (Teiidae) on Sint Eustatius, Netherlands Antilles: Baseline data on a small population in a severely altered habitat. *Carib. J. Sci.* **41**, 162–169.
- Kolbe, J.J., Colbert, P.L., & Smith, B.E. (2008).

- Niche relationships and interspecific interactions in Antigua lizard communities. *Copeia* **2008**, 261–272.
- Lewis, A.R. & Saliva, J.F. (1987). Effects of sex and size on home range, dominance and activity budgets in *Ameiva exsul* (Lacertilia: Teiidae). *Herpetologica* **43**, 374–383.
- Losos, J.B. (2009). *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. Berkeley, Univ. California Press. xx + 507 pp.
- Malhotra, A. & Thorpe, R.S. (1999). *Reptiles & Amphibians of the Eastern Caribbean*. London, Macmillan Educ. Ltd. ix + 134 pp.
- Meier, A.J. & Noble, R.E. (1991). Notes on the natural history of *Anolis desechensis*. *Florida Fld. Nat.* **19**, 17–18.
- Meier, A.J., Noble, R.E., & Rathbun, S.L. (1993). Population status and notes on the biology of the St. Croix Ground Lizard on Green Cay (St. Croix, U. S. Virgin Islands). *Carib. J. Sci.* **29**, 147–152.
- Micco, S.M., Lahey, G.J., Sosa, R.A., Powell, R., Censky, E.J., & Parmerlee, J.S., Jr. (1997). Natural history of *Leiocephalus barahonensis* (Tropiduridae) on the Península de Barahona, Hispaniola: An examination of two populations. *Herpetol. Nat. Hist.* **5**, 147–156.
- Regal, P.J. (1978). Behavioural differences between reptiles and mammals: An analysis of activity and mental capabilities. In: *Behaviour and Neurology of Lizards: An Interdisciplinary Colloquium*, pp. 183–202. Greenberg, N., MacLean, P.D. (Eds.). Rockville, Maryland, Nat. Inst. Mental Health.
- Regal, P.J. (1983). The adaptive zone and behaviour of lizards. In: *Lizard Ecology: Studies of a Model Organism*, pp. 105–118. Huey, R.B., Pianka, E., Schoener, T.W. (Eds.). Cambridge, Massachusetts, Harvard Univ. Press.
- Schell, P.T., Powell, R., Parmerlee, J.S., Jr., Lathrop, A., & Smith, D.D. (1993). Notes on the natural history of *Ameiva chrysolema* (Sauria: Teiidae) from Barahona, Dominican Republic. *Copeia* **1993**, 859–862.
- Simmons, P.M., Greene, B.T., Williamson, K.E., Powell, R., & Parmerlee, J.S., Jr. (2005). Ecological interactions within a lizard community on Grenada. *Herpetologica* **61**, 124–134.
- Vitt, L.J. & Colli, G.R. (1994). Geographical ecology of a Neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. *Can. J. Zool.* **72**, 1986–2008.
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