HERPETOZOA 22 (3/4): 167 - 171
Wien, 30. Dezember 2009

Foraging behavior of the lizard *Ameiva erythrocephala* DAUDIN, 1802
(Squamata: Sauria: Teiidae)

Das Beuteverhalten von *Ameiva erythrocephala* DAUDIN, 1802
(Squamata: Sauria: Teiidae)

VICTORIA H. ZERO & DOUGLAS A. EIFLER & ROBERT POWELL

KURZFASSUNG

Die Autoren beschreiben das Beuteverhalten des Teiiden *Ameiva erythrocephala* DAUDIN, 1802 in zwei Lebensräumen. Gezielte Beobachtungen über insgesamt 6,7 Stunden zeigten, daß die Tiere bei der Nahrungssuche eine Kombination aus häufigen Ortswechseln und Grabphasen anwendeten. Futtersuchende *A. erythrocephala* bewegten sich im Durchschnitt 26% der Zeit fort und führten im Mittel 2,36 Ortswechsel pro Minute aus. Ebenfalls dokumentiert wurden die Dauer von Fortbewegungs- und Grabphasen sowie der grabend verbrachten Zeit und die Häufigkeit von Grabphasen. Häufigkeit von Ortswechseln und Dauer der Fortbewegungsphasen waren im Lebensraum Wald positiv mit der Kopf-Rumpf-Länge korreliert. Bei Tieren des Buschlandes war die Dauer der einzelnen Fortbewegungsphasen kürzer und die Häufigkeit der Grabphasen größer als bei denen des Waldes.

ABSTRACT

We characterized foraging behaviors for the teiid lizard *Ameiva erythrocephala* DAUDIN, 1802 in two habitats. Focal observations totaling 6.7 hours indicated that individuals searched for food through a combination of frequent moves and digging bouts. Foraging *A. erythrocephala* moved 26% of the time, on average, and moved an average of 2.36 times per minute. We also documented the move and dig durations, time spent digging, and digging rate. Movement rate and move duration were positively correlated with snout-vent length (SVL) at the forest site. Lizards in scrub habitats made shorter individual moves and dug more frequently than those in forested habitats.

KEY WORDS

Reptilia: Squamata: Sauria: Teiidae: *Ameiva erythrocephala*; search behavior, ethology, foraging, diet, digging behavior, ontogenetic shifts in diet and foraging, St. Eustatius (Netherlands Antilles)

INTRODUCTION

Foraging strategies of animals are often described as fitting into one of two distinct categories: Either sit-and-wait or widely foraging (e.g., PIANKA 1966; HUEY & PIANKA 1981; VITT & PRICE 1982). The taxonomic distribution of these foraging strategies is influenced largely by phylogeny (COOPER 1995; PERRY 1999). Variation in foraging strategy within a clade becomes important for understanding the environmental forces that shape foraging behavior (O'BRIEN et al. 1990).

Foraging behavior among related lizard species is highly stable, with close relatives typically exhibiting the same general foraging style (COOPER 1994a, 1994b, 1995). Infrequently, distinct foraging styles may be used by closely related species or within a species (COOPER & WHITING 2000). Intraspecifically, lizard foraging may vary depending on gender (DURTSCHE 1992; LISTER & AGUAYO 1992; PERRY 1996; EIFLER & EIFLER 1999), and age or size (TAYLOR 1986; PAULISSEN 1987a; WIKELSKI & TRILLMICH 1994; PERRY 1996; GREEFF & WHITING 2000; KEREN-ROTEM et al. 2006). Habitat variation also may substantially affect foraging behaviors. For example, Northern Wheatears (*Oenanthe oenanthe*) shift foraging mode in relation to density and height of vegetation (EXNEROVA et al. 2002). Interspecific variation in *Anolis* lizard foraging is associated with variation in habitat structure (MOERMOND 1979). Although habitat heterogeneity has not been well documented as a source of intraspecific variation in foraging lizards, it appears to be important in determining the foraging behavior of at least some species.

The paraphyletic lizard genus *Ameiva* (Teiidae; REEDER et al. 2002) includes 32 currently recognized species (HOWER & HEDGES 2003), which are widely distributed in continental Central and northern South America, and in the West Indies. Twenty-two species occur in the West Indies, and many are endemic (SCHWARTZ & HENDERSON 1991; HENDERSON & POWELL 2009). They are generally shorter than 16 cm in snout-vent length (SVL), with a range from 4 cm (*Ameiva wetmorei* STEJNEGER, 1913) to 20 cm (*Ameiva exsul* COPE, 1863 and *Ameiva fuscata*; GARMAN, 1887) (HENDERSON & POWELL 2009). They occupy a wide range of habitats that include open savannahs, tropical forests, sandy beaches, and even suitable areas in more urban regions. These diurnal lizards typically forage on the ground, using a well-developed sense of smell to actively search for prey both above and below the surface. Their diet consists primarily of arthropods, with vertebrates and fruit included in the diet of some species (SCHWARTZ & HENDERSON 1991; ZALUAR & ROCHA 2000; HENDERSON & POWELL 2009). *Ameiva* are prey of numerous species, including snakes, other lizards, and birds. As a group, they are typically described as active foragers that spend relatively large proportions of time in motion and make frequent moves per minute (MAGNUSSON et al. 1985; LEWIS & SALIVA 1987; PERRY 1999; SIMMONS et al. 2005; RUDMAN et al. 2009).

Our purpose in this study was to characterize the foraging behavior of *Ameiva erythrocephala* DAUDIN, 1802. In particular we sought to identify ontogenetic trends and habitat-based variation in foraging behavior. *Ameiva erythrocephala* is a medium-sized teiid lizard (SVL <14 cm) endemic to the St. Christopher Bank, Lesser Antilles (KERR et al. 2006). Although apparently restricted to areas with heavy human traffic on mongoose-infested St. Christopher and Nevis (BARBOUR 1930; WESTERMAN 1953; POWELL & HENDERSON 2005), these lizards are abundant on mongoose-free St. Eustatius, where they occur in a number of habitats that include *Acacia* scrub, xeric woodlands, rocky beaches, and human-modified areas (KERR et al. 2005; POWELL et al. 2005; HENDERSON & POWELL 2009).

METHODS

We studied *A. erythrocephala* from 12–22 June 2004 on Gilboa Hill, St. Eustatius, Netherlands Antilles (17°30'N, 63° 30'W). Focal animal observations were conducted from 09:00–16:00 h on warm sunny days. Nine lizards were observed on an east-facing slope (Site 1), characterized by xeric scrub dominated by *Acacia* spp. (Fabaceae) and *Jatropha gossypifolia* (Euphorbiaceae), although the site contained areas of closed canopy forest with a leaf litter layer and unvegetated bare ground. Nineteen animals were observed on a north-facing slope (Site 2), characterized by broadleaf xeric forest with an almost continuous closed canopy, little understory vegetation, and a relatively uniform leaf litter layer. The sites were separated by a distance of ~150 m. We did not observe movement of marked animals between sites.

At Site 1, animals were captured (by noosing) at least one day prior to observations, measured (SVL), and uniquely marked with nontoxic paint. Animals at Site 2 were not captured. After a lizard was observed at Site 2, it was sprayed with acrylic latex paint (diluted 1:1) to avoid repeated observations of individuals. Two lizards escaped before being sprayed, and they may have been observed more than once. For Site 2 lizards, SVL was estimated to the nearest centimeter.

We observed each lizard for 8.37–19.27 minutes, locating them by walking slowly through the study sites. When a lizard was detected, the observer stopped moving immediately to minimize disturbance. Lizards were generally observed from distances >5 m, but some individuals were discovered and observed at considerably closer distances (<2 m). Lizards appeared undisturbed by our presence as long as we remained motionless. Data were recorded on an HP 200LX® Palmtop computer (Hewlett-Packard Development Co., Palo Alto, California, USA).

We recorded the duration of each movement and each digging event. For movements, we recorded only instances when the lizard moved more than one body length. Digging events were recorded whenever a lizard dug at the surface with its front limbs. Any apparent pause in digging motion of any duration indicated the end of a digging event. Six measures of foraging activity were generated: movements per minute (MPM), proportion of time spent moving (PTM; e.g., HUEY & PIANKA 1981; COOPER et al. 1997; PERRY 1999), movement duration (MD), digging events per minute (DPM), proportion of time spent digging (PTD), and duration of digging events (DD). All focal observations were performed by VHZ.

We generated a mean value for our six measures for each animal. We used StatView 5.0® (SAS Institute Inc., Cary, North Carolina, USA) for statistical analyses: non-parametric Mann-Whitney U tests for comparisons between sites and simple regression to examine relationships between foraging parameters and lizard body sizes. All means are reported ± one standard deviation (SD), followed by range in parentheses.

RESULTS

Our nine Site 1 animals had an average SVL of 7.6±2.2 cm (4.4–11.4 cm). Lizards were observed for an average of 12.75±2.52 min (8.8–15.68 min). Neither our movement measurements nor our digging data were significantly related to body size at this site (MPM: $F_8 = 1.07$, $P = 0.34$; PTM: $F_8 = 0.48$, $P = 0.51$; MD: $F_8 = 1.33$, $P = 0.29$; DPM: $F_8 = 0.02$, $P = 0.90$; PTD: $F_8 = 1.48$, $P = 0.26$; DD: $F_8 = 1.51$, $P = 0.26$; Table 1).

The 19 animals in Site 2 had an average SVL of 6.8±1.7 cm (4–11 cm). Lizards were observed for an average of 9.13±2.6 min (8.37–19.27 min). Larger animals moved more frequently ($F_{18} = 4.65$, $r^2 = 0.22$, $P = 0.046$; Table 1) and spent more time moving ($F_{18} = 5.92$, $r^2 = 0.26$, $P = 0.026$; Table 1). However, no significant relationship was found between body size and movement duration ($F_{18} = 0.11$, $P = 0.74$; Table 1) or digging (DPM: $F_{18} = 0.01$, $P = 0.92$; PTD: $F_{18} = 0.05$, $P = 0.83$; DD: $F_{18} = 0.47$, $P = 0.50$; Table 1).

Lizard movements lasted longer at Site 2 than Site 1 (Mann-Whitney U: $U_{19,9} = 9.5$, $P = 0.0002$). No significant differences were found for MPM or PTM (MPM: $U_{19,9} = 60$, $P = 0.21$; PTM: $U_{19,9} = 62$, $P = 0.25$). Site 1 animals dug more frequently ($U_{19,9} = 35$, $P < 0.0130$). The proportion of time digging and duration of digging episodes was comparable between sites (PTD: $U_{19,9} = 62$, $P = 0.24$; DD: $U_{19,9} = 81$, $P = 0.82$). All feeding events appeared to involve lepidopteran or coleopteran larvae, except for one individual in Site 1 that ate a cockroach (Blattodea) that crossed its path.

Table 1: Summary statistics for measures of foraging behavior in *Ameiva erythrocephala* DAUDIN, 1802 in two habitats on St. Eustatius, Netherlands Antilles: MPM – movements per minute, PTM – proportion of time moving (%), MD – duration of moving events (sec), DPM – digs per minute, PTD – proportion of time digging (%), DD – duration of digging events (sec).

Tab. 1: Beschreibende Statistiken (arithmetischer Mittelwert ± Standardabweichung, Spannweite in Klammern) zum Beuteverhalten von *Ameiva erythrocephala* DAUDIN, 1802 in zwei Lebensräumen (Site 1 – Buschland, Site 2 – Wald) auf St. Eustatius, Niederländische Antillen: MPM – Ortswechsel pro Minute, PTM – zeitlicher Anteil von Bewegungsphasen (%), MD – Dauer der einzelnen Bewegungsphase (sec), DPM – Grabphasen pro Minute, PTD – zeitlicher Anteil der Grabphasen (%), DD – Dauer der einzelnen Grabphase (sec).

Variable	Scrub Habitat, Site 1 ($n = 9$) ± SD (range)	Forest habitat, Site 2 ($n = 19$) ± SD (range)	Site 1 + Site 2 Combined ± SD (range)
MPM	2.90 ± 1.76 (0.30–6.17)	2.10 ± 0.81 (0.95–4.64)	2.36 ± 1.23 (0.30–6.17)
PTM	0.21 ± 0.12 (0.02–0.40)	0.28 ± 0.11 (0.14–0.62)	0.26 ± 0.11 (0.02–0.62)
MD	4.68 ± 0.76 (3.80–6.00)	8.22 ± 2.51 (5.10–14.70)	7.08 ± 2.69 (3.80–14.70)
DPM	0.73 ± 0.25 (0.22–1.03)	0.40 ± 0.30 (0.00–0.98)	0.50 ± 0.32 (0.00–1.03)
PTD	0.20 ± 0.13 (0.06–0.44)	0.16 ± 0.16 (0.00–0.45)	0.18 ± 0.15 (0.00–0.45)
DD	17.67 ± 11.00 (5.80–37.40)	21.01 ± 15.50 (1.60–68.84)	19.90 ± 14.02 (1.60–68.84)

DISCUSSION

Our data suggest that *A. erythrocephala* uses a foraging strategy similar to that described in congeners. Previous studies of foraging in species of *Ameiva* generated MPM of 0.58–5.6 and PTM of 0.26–0.51 (MAGNUSSON et al. 1985; LEWIS & SALIVA 1987; PERRY 1999; SIMMONS et al. 2005; RUDMAN et al. 2009). Our data for lizards occupying the forested north-facing slope were suggestive of ontogenetic shifts in foraging, with larger animals moving more frequently and for longer durations. This pattern might be prompted by size-related changes in diet. Insectivorous lizards often exhibit ontogenetic shifts in diet, wherein larger individuals incorporate larger prey types into their diets and smaller types are dropped (PAULISSEN 1987b; ZALUAR & ROCHE 2000), although many West Indian lizards, regardless of age or size, feed on small items such as ants or termites (HENDERSON & POWELL 2009). However, consumption of social insects, even if small in size, is "economically feasible because they normally occur in a clumped spatial distribution and hence constitute a concentrated food supply" (PIANKA 1986). Differences in prey size, availability, and detectability can lead to modifications in search strategy (PAULISSEN 1987a; O'BRIEN et al. 1990). More detailed data on the diet of *A. erythrocephala* are needed to evaluate the applicability of the trend apparent in our data.

Variation in foraging behavior also might be attributable to differences in habitats. Animals at the forested site made longer individual moves than those at the scrub site, where animals dug more frequently. Although our sample sizes are small, these data suggest that *A. erythrocephala* adjusts its behavior in response to environmental variation. However, we cannot determine what aspects of the environment might be important, as the differences in foraging behavior between sites could be attributable to any number of variables, including prey availability, habitat structure, or even predation risk. Additional data documenting variation in foraging behavior are necessary for identifying the environmental factors that might influence behavior in *A. erythrocephala*.

ACKNOWLEDGEMENTS

Ellen CENSKY (Milwaukee Public Museum), Trevor JOYCE (University of Alaska Southeast), and Sean FOGARTY (Harvey Mudd College) helped in the field. Robert HENDERSON (Milwaukee Public Museum) and Maria EIFLER (Erell Institute) provided invaluable comments. Permits were provided by the St. Eustatius National Parks Foundation (STENAPA). Research was supported by National Science Foundation Grant No. DBI-9732257 to RP.

REFERENCES

BARBOUR, T. (1930): Some faunistic changes in the Lesser Antilles.– Proceedings of the New England Zoölogical Club, Cambridge, MA; 11: 73–85.

COOPER, Jr., W. E. (1994a): Prey chemical discrimination, foraging mode, and phylogeny; pp. 1–16. In: VITT, L. J. & PIANKA, E. R. (eds.): Lizard ecology: historical and experimental perspectives; Princeton, New Jersey (Princeton Univ. Press).

COOPER, Jr., W. E. (1994b): Chemical discrimination by tongue-flicking lizards: A review with hypotheses on its origin and its ecological and phylogenetic relationships.– Journal of Chemical Ecology, New York, NY; 20: 439–487.

COOPER, Jr., W. E. (1995): Foraging mode, prey chemical discrimination, and phylogeny in lizards.– Animal Behaviour, Amsterdam, The Netherlands; 50: 973–985.

COOPER, W. E., Jr. & WHITING, M. J. (2000): Ambush and active foraging modes both occur in the scincid genus *Mabuya*.– Copeia, Lawrence, KS; 2000: 112–118.

COOPER, W. E., Jr. & WHITING, M. J. & VAN WYK, J. H. (1997): Foraging modes of cordyliform lizards.– South African Journal of Zoology, Pretoria; 32: 9–13.

DURTSCHE, R. D. (1992): Feeding time strategies of the fringe-toed lizard, *Uma inornata* during breeding and non-breeding seasons.– Oecologia, Berlin/Heidelberg; 89: 85–89.

EIFLER, D. A. & EIFLER, M. A. (1999): The influence of prey distribution on the foraging strategy of the lizard *Oligosoma grande* (Reptilia: Scincidae).– Behavioral Ecology and Sociobiology, New York, NY; 45: 397–402.

EXNEROVA, A. & JAROSIK, V. & KRISTIN, A. (2002): Variation in foraging mode of the Northern Wheatear (*Oenanthe oenanthe*).– Ardea, Leiden, The Netherlands; 90: 275–284.

Greeff, J. M. & Whiting, M. J. (2000): Foraging-mode plasticity in the lizard *Platysaurus broadleyi*.– Herpetologica, Lawrence, KS; 56: 402–407.

Henderson, R. W. & Powell, R. (2009): Natural history of West Indian reptiles and amphibians; Gainesville (University Press of Florida); XXIV, 495 pp.

Hower, L. M. & Hedges, S. B. (2003): Molecular phylogeny and biogeography of West Indian teiid lizards of the genus *Ameiva*.– Caribbean Journal of Science, Mayagüez, Puerto Rico; 39: 298–306.

Huey, R. B. & Pianka, E. R. (1981): Ecological consequences of foraging mode. Ecology, Ithaca, NY; 62: 991–999.

Keren-Rotem, T. & Bouskila, A. & Geffen, E. (2006): Ontogenetic habitat shift and risk of cannibalism in the Common Chameleon (*Chamaeleo chamaeleon*).– Behavioral Ecology and Sociobiology, New York, NY; 59: 723–731.

Kerr, A. M. & Powell, R. & Parmerlee, J. S., Jr. (2005): *Ameiva erythrocephala* (Teiidae) on Saint Eustatius, Netherlands Antilles: Baseline data on a small population in a severely altered habitat.– Caribbean Journal of Science, Mayagüez, Puerto Rico; 41: 162–169.

Kerr, A. M. & Zero, V. H. & Powell, R. (2006): *Ameiva erythrocephala*.– Catalogue of American Amphibians and Reptiles, Salt Lake City, UT; 817: 1–4.

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, Lawrence, KS; 43: 93–98.

Lister, B. C. & Aguayo, A. G. (1992): Seasonality, predation, and the behavior of a tropical mainland anole.– Journal of Animal Ecology, London, United Kingdom; 61: 717–733.

Magnusson, W. E. & Paiva, I. J. & Rocha, R. M. & Franke, C. R. & Kasper, L. A. & Lima, A. P. (1985): The correlates of foraging made in a community of Brazilian lizards.– Herpetologica, Lawrence, KS; 41: 324–332.

Moermond, T. C. (1979): The influence of habitat structure on *Anolis* foraging behavior.– Behaviour, Leiden, The Netherlands; 70: 147–167.

O'Brien, W. J. & Browman, H. I. & Evans, B. I. (1990): Search strategies of foraging animals.– American Scientist, Research Triangle Park, NC; 78: 152–160.

Paulissen, M. A. (1987a): Optimal foraging and intraspecific diet differences in the lizard *Cnemidophorus sexlineatus*.– Oecologia, Berlin/Heidelberg; 71: 439–446.

Paulissen, M. A. (1987b): Diet of adult and juvenile Six-lined Racerunners, *Cnemidophorus sexlineatus* (Sauria: Teiidae).– Southwestern Naturalist, Norman, OK; 32: 395–397.

Perry, G. (1996): The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behavior and diet.– Canadian Journal of Zoology, Toronto; 74: 1238–1245.

Perry, G. (1999): The evolution of search modes: ecological versus phylogenetic perspectives.– American Naturalist, Chicago, IL; 153: 98–109.

Pianka, E. R. (1966): Convexity, desert lizards, and spatial heterogeneity.– Ecology, Ithaca, NY; 47: 1055–1059.

Pianka, E. R. (1986): Ecology and natural history of desert lizards; Princeton, New Jersey (Princeton University Press).

Powell, R. & Henderson, R. W. (2005): Conservation status of Lesser Antillean reptiles.– Iguana, San Jose, CA; 12: 62–77.

Powell, R. & Henderson, R.W. & Parmerlee, J. S., Jr. (2005): Reptiles and amphibians of the Dutch Caribbean: St. Eustatius, Saba, and St. Maarten; Gallows Bay, St. Eustatius, Netherlands Antilles (St. Eustatius National Parks Foundation).

Reeder, T. W. & Cole, C. J. & Dessauer, H. C. (2002): Phylogenetic relationships of whiptail lizards of the genus *Cnemidophorus* (Squamata: Teiidae): a test of monophyly, reevaluation of karyotypic evolution, and review of hybrid origins.– American Museum Novitates, New York, NY; 3365: 1–61.

Rudman, S.M. & Powell, R. & Parmerlee, J. S., Jr. (2009): *Ameiva fuscata* on Dominica, Lesser Antilles: natural history and interactions with *Anolis oculatus*.– Herpetological Bulletin, Montrose, United Kingdom; 109, in press.

Schwartz, A. & Henderson, R. W. (1991): Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history; Gainesville (University of Florida Press), XVI, 720 pp..

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, Lawrence, KS; 61: 124–134.

Taylor, J. A. (1986): Food and foraging behaviour of the lizard, *Ctenotus taeniolatus*.- Australian Journal of Ecology, Oxford, United Kingdom; 11: 49–54.

Vitt, L. J. & Price, H. J. (1982): Ecological and evolutionary determinants of relative clutch mass in lizards.– Herpetologica, Lawrence, KS; 38: 237–255.

Westerman, J. H. (1953): Nature preservation in the Caribbean. A review of literature on the destruction and preservation of flora and fauna in the Caribbean area.– Publication of the Foundation for Scientific Research in Surinam and the Netherlands Antilles, Utrecht, The Netherlands; 9: 1–107.

Wikelski, M. & Trillmich, F. (1994): Foraging strategies of the Galapagos Marine Iguana (*Amblyrhynchus cristatus*): adapting behavioural rules to ontogenetic size change.– Behaviour, Leiden, The Netherlands; 128: 255–279.

Zaluar, H. L. T. & Rocha, C. F. D. (2000): Ecology of the wide-foraging lizard *Ameiva ameiva* (Teiidae) in a sand dune habitat of Southeast Brazil: ontogenetic, sexual and seasonal trends in food habits, activity, thermal biology and microhabitat use.– Ciência e Cultura (Journal of the Brazilian Association for the Advancement of Science), São Paulo; 52: 101–107.

DATE OF SUBMISSION: July 6, 2009 Corresponding editor: Heinz Grillitsch

AUTHORS: Victoria H. Zero, Department of Biology, Reed College, Portland, Oregon 97202, USA; Douglas A. Eifler, USDA Forest Service Liaison's Office, Haskell Indian Nations University, Box 5018, 155 Indian Ave., Lawrence, KS 66046, USA; Robert Powell (corresponding author), Department of Biology, Avila University, Kansas City, Missouri 94145, USA < robert.powell@avila.edu >

Zeitschrift/Journal: Herpetozoa

Jahr/Year: 2010

Band/Volume: 22_3_4

Autor(en)/Author(s): Zero Victoria, Eifler Douglas A., Powell Robert

Artikel/Article: Das Beuteverhalten von Ameiva erythrocephala DAUDIN, 1802 (Squamata: Sauria: Teiidae) 167-171