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Ecological Performance in the Actively Foraging Lizard *Ameiva ameiva* (Teiidae)

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ABSTRACT.—We examined maximal and ecological performance in *Ameiva ameiva* on Union Island, St. Vincent and the Grenadines. Maximal sprint speed was correlated positively with lizard body size but not with hind-limb or relative hind-limb length. Lizards in the field used over 85% of maximal capacity when escaping a putative predator, and the proportion of maximal speed used was highly dependent on behavioral context. Mean and median speeds used by adults when moving undisturbed through the habitat were 15.37 ± 2.01 (SE) and 11.41% of maximal speed; and approximately 65% of undisturbed movement is at speeds <15% of maximal capacity. No individual movement exceeded 40% of maximal capacity. Mean and median values for distances moved were 7.88 ± 0.72 (SE) and 8.14 cm, with 91% of distances moved <12 cm and 69.5% <10 cm, demonstrating that undisturbed lizards move through their habitat using short individual movements at low speeds. Similar to other studies on primarily sedentary lizards, actively foraging lizards may experience stronger natural selection on locomotor speed when evading a predator rather than while foraging because these lizards use nearly 90% of their maximal capacity during the former activity.

In recent years, researchers increasingly have focused attention on how organisms perform in their natural habitats and how the magnitude of this performance relative to putatively maximal capacities differs among behavioral contexts (Irschick and Losos, 1998; Irschick, 2000a,b). “Maximal performance” is defined as the maximal ability of an organism to accomplish an ecological task using dynamic motion (e.g., biting, running, flying, or swimming), and “ecological performance” refers to how an organism uses its maximal performance in nature while accomplishing an ecological task (Irschick and Garland, 2001; Irschick, 2003). In the field, animals are predicted to perform at near-maximal capacities in situations that are critical to fitness (e.g., when escaping from predators or defending territories [Husak et al., 2008]). Movements at these near-maximal speeds occur with relatively low frequency in nature, because they are energetically unsustainable in the long term. Slower movements are frequently used in other behavioral contexts, such as while feeding or moving undisturbed through the habitat. Thus, in many organisms, locomotion generally occurs over a relatively narrow range of speeds (i.e., preferred speed; Pennycuik, 1975; Hoyt and Taylor, 1981; Perry et al., 1988; Irschick, 2000b).

Ecological and maximal performances are perhaps best studied in lizards. The proportion of maximal locomotor capacity used in nature varies with respect to behavior and ontogeny (Irschick, 2000b). In *Anolis* lizards, all age classes use a significantly lower proportion of maximal capacity when moving undisturbed through their habitat than when fleeing from a predator. In addition, despite lower absolute maximal sprinting capacities, juvenile *Anolis* lizards typically use a higher proportion of their maximal speeds when escaping a threat than adults (Irschick and Losos, 1998; Irschick, 2000a). A similar pattern of contextual use of locomotor capacity was observed in Eastern Collared Lizards, *Crotaphytus collaris* (Husak and Fox, 2006), and field use of maximal speed when escaping a predator has been shown to enhance survival (Husak, 2006).

Despite the clear importance of examining both maximal and ecological performance, data are available for only a few groups of lizards (Irschick and Losos, 1998; Irschick, 2000a; Irschick et

al., 2005; Husak and Fox, 2006). In this study, we add to this database by examining maximal and ecological performances in *Ameiva ameiva*, a widely foraging teiid lizard found in northern South America and a few southern Lesser Antillean islands. Specifically, we address the following questions: (1) Does *A. ameiva* move at different speeds during different behaviors? (2) Does it use near maximal capacities when escaping from predators? (3) What percentage of average maximal locomotor capacities does *A. ameiva* use in the field when moving undisturbed? (4) How does actively foraging *A. ameiva* compare to other species of lizards in respect to the distributions of speeds used and distances moved while undisturbed in nature?

MATERIALS AND METHODS

General Methods.—The study site was an approximately 0.57-ha area near Clifton, Union Island, St. Vincent and the Grenadines. The site was characterized by thorny scrub (*Acacia* sp.) that accounted for 60–80% of total canopy cover and coastal *Coccoloba uvifera*, the canopy of which comprised <20% of the total. Total canopy height was <3 m. We captured adult lizards using a noose and immediately recorded cloacal temperatures using a quick-reading electronic thermometer with a type K thermocouple (Fluke Corp., Everett, WA). We measured snout–vent lengths (SVL) and tail lengths to the nearest millimeter using a clear plastic ruler, mass to the nearest gram with a 60-g Pesola® spring scale (Pesola AG, Baar, Switzerland) and hind-limb length to the nearest 0.01 mm using electronic calipers (Mitutoyo Corp., Aurora, IL). We determined sex and marked each animal uniquely with nontoxic paint.

Maximal Sprint Speed.—We quantified maximal sprint speed for 12 lizards (9 males, 2 females, 1 subadult) using high-speed video. All lizards had intact or fully regenerated tails. Each lizard was tested three times with a minimum of 1-h rest between trials. Prior to each trial, we painted a white dot on the side of the head of each animal to facilitate tracking in the videos. We placed lizards in cloth bags in filtered sunlight for approximately 30 min to attain a desired test temperature within the set-point range (37.4–39.0°C). Mean body temperature of lizards during all trials was $38.5 \pm 0.4^\circ\text{C}$, which closely approximates the lizards’ preferred temperatures determined in a laboratory thermal gradient (mean \pm SEM = $38.31 \pm 0.89^\circ\text{C}$; D. N. Muñiz Pagan,

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unpubl. data). We constructed a 175-cm long outdoor racetrack on a natural substrate of sand with a clear glass wall marked at 25-cm intervals. Each trial was digitally recorded at 300 frames per second (fps) using a Casio Exilim FX-1 camera (Casio Computer Co., Ltd., Tokyo). Later we viewed the recordings and counted the number of frames necessary for each lizard to traverse 25-cm intervals. Each trial produced multiple 25-cm bursts (2–5 bursts, 3.36 ± 1), and the maximum velocity recorded over all bursts and trials was taken as the maximum for that animal.

Ecological Performance.—We quantified ecological performance using the methods of Irschick and Losos (1998) and Husak and Fox (2006). In the field, we digitally recorded 21 different adult individuals at 30 fps during peak activity (0800–1400 h; D. N. Muñiz Pagan, unpubl. data). We focused on two behaviors, undisturbed movement and predator escape. Twelve animals were recorded during undisturbed locomotion (foraging) and nine while responding to a putative predator. For the latter, one person (the same person for all trials wearing similar clothing) approached a lizard at a constant pace of approximately 40 m/sec (e.g., Cooper, 1997). At the end of each recording, we placed an object of known length in the frame where the lizard was first observed to serve as a scale to calibrate videos. Videos were calibrated to known scale and digitized using Image J (National Institutes of Health, Bethesda, MD; <http://rsbweb.nih.gov/ij/>). We calculated the maximum velocity over approximately 20 cm for predator escape trials (mean \pm SEM = 23.6 ± 7.0 cm) and over approximately 10 cm for undisturbed/foraging movements (11.6 ± 7.0 cm). We chose the former distance to be comparable to our maximal speed measurements. A shorter distance was used for the latter behavior because the natural movements of these lizards consisted of short starts and stops, with movements averaging approximately 10 cm. We were unable to capture most animals after ecological performance trials; therefore, for each animal, the proportion of maximal speed used in nature was calculated using the mean maximal speed measured in the racetrack (e.g., Irschick, 2000a).

Statistical Analysis.—All morphological and locomotion data were \log_{10} -transformed prior to analysis. Laboratory measurements of sprinting speed are dependent on variations in motivation and the responses of animals to present environmental stimuli (VanBerkum and Tsuji, 1987; Losos et al., 2002). Therefore, we assessed repeatability of our sprint-speed measurements by calculating Pearson product-moment correlations (Hayes and Jenkins, 1998) between the best and second-best measurements for each individual.

To determine whether *A. ameiva* uses speed differently depending on behavioral context, we used one-way ANOVA with behavioral context as the sole independent variable (undisturbed vs. escape) and speed as the dependent variable (absolute speed and proportion of maximal speed). For comparison with other studies, we also explored the entire distribution of speeds and distances moved by lizards during undisturbed locomotion. We used JMP 7.0.2 (SAS Institute, Cary, NC) for statistical analyses. All means are presented \pm SE (except as indicated). For all statistical tests, $\alpha = 0.05$.

RESULTS

Maximal Sprint Speed.—Maximal sprint speed measured in the racetrack proved to be highly repeatable ($r = 0.98$, $P < 0.001$). Sprint speed was correlated positively with lizard body size ($F_{1,11} = 5.47$, $P = 0.04$) but not with either hind-limb length ($F_{1,11} =$

TABLE 1. Speeds of movement (cm s^{-1}) for *Ameiva ameiva* on a racetrack (maximal sprint speed) during escapes in the field and while moving undisturbed and presumably foraging.

	N	Mean \pm SE	Range
Maximum	12	219.0 \pm 12.5	157.8–291.4
Escape	9	192.4 \pm 16.8	111.3–242.1
Undisturbed	12	50.4 \pm 8.43	11.8–106.7

3.90, $P = 0.08$) or relative hind-limb length ($F_{1,11} = 0.058$, $P = 0.81$). Because only two females were included in our sample, data were insufficient for comparing sizes and sprint speeds among sexes.

Ecological Performance.—We recorded no overlap in the distributions of speeds used during escapes and undisturbed movement/foraging in the field, nor did we record any overlap between the distributions of maximum (i.e., racetrack) speeds and those recorded during undisturbed movements (Table 1). *Ameiva ameiva* used significantly faster sprint speeds when escaping a putative predator than when moving undisturbed through the habitat ($F_{1,20} = 45.79$, $P < 0.0001$). Thus, the proportion of maximal speed used was highly dependent on behavioral context (escapes, $87.8 \pm 23.0\%$; undisturbed, $23.0 \pm 13.3\%$; $F_{1,20} = 66.31$, $P < 0.0001$). Moreover, maximal speed did not differ significantly from speeds used when escaping a predator ($F_{1,20} = 1.69$, $P = 0.21$).

Speed and Distance Moved Distributions.—All movements, regardless of distance traveled, were used to calculate speed and distance moved distributions. Mean and median speeds used by adult *A. ameiva* while moving undisturbed through the habitat were 15.37 ± 2.01 (SE) and 11.41, respectively, for percent maximal speed (Fig. 1A). Approximately 65% of the total distribution of undisturbed movement occurs at speeds less than 15% of maximal capacity, and no individual movement exceeded 40% of maximal capacity. Mean and median values for distances moved were 7.88 ± 0.72 (SE) and 8.14 cm, respectively. Similar to speeds used, the range of distances moved was narrow (Fig. 1B), with 91% of the entire distribution less than 12 cm, and 69.5% less than 10 cm. Thus, *A. ameiva* tended to move through the habitat using short individual movements (~ 8 cm) at low speed (mean = 34.12 cm s^{-1}).

DISCUSSION

Maximal sprinting capacity is a performance variable with a long history of scrutiny in the literature because fast bursts of speed are likely important for evading predators, obtaining resources, and defending territories (Bennett, 1980; Jayne and Bennett, 1990; Le Galliard et al., 2004; Miles, 2004; Husak et al., 2006). Thus, maximal sprinting speed is thought to be an ecologically relevant trait related to fitness. However, recent studies have suggested that fitness may not always be related to how fast an organism can run but instead how fast they actually run in nature (i.e., ecological performance; Husak, 2006; Irschick et al., 2005). To date, patterns of ecological performance are available for only a few groups of lizards, and no data are available for teiids, a group of predominantly active foragers.

Similar to other lizards examined to date, we found that ecological performance in *A. ameiva* is highly dependent on behavioral context. When escaping a predator, *A. ameiva* engages in very rapid bursts of locomotion and uses a large proportion of their maximal sprinting capacity (87.8%). In contrast, while moving undisturbed through their environment

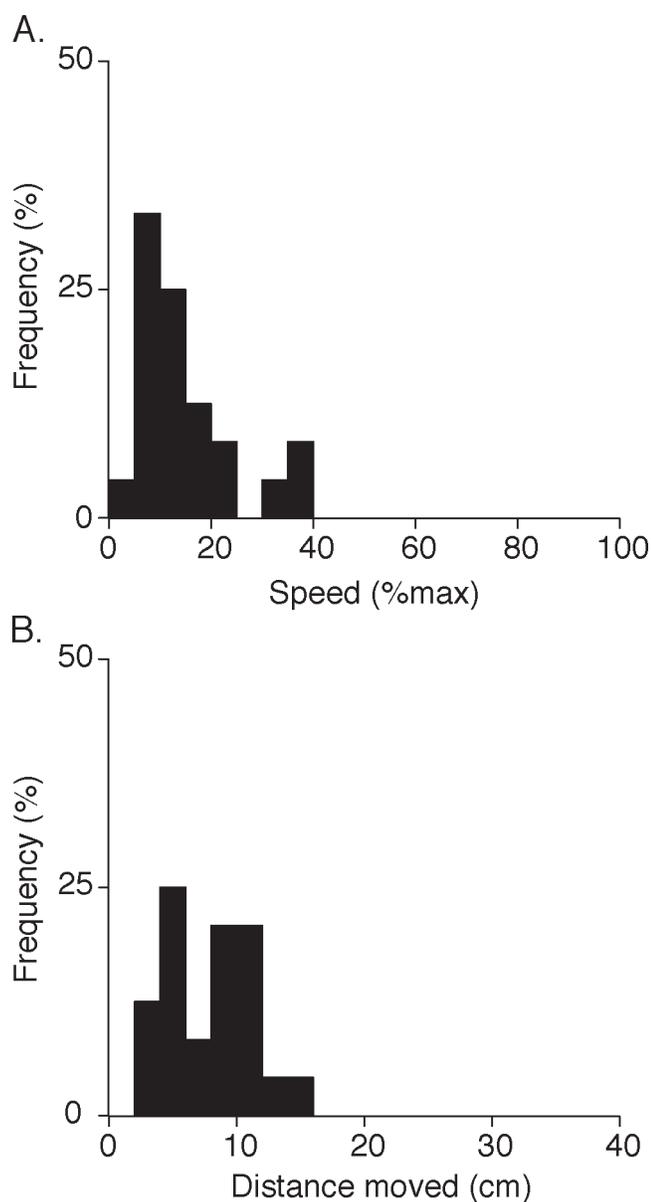


FIG. 1. Frequencies of speeds used (A) and distances moved (B) by adult *Ameiva ameiva* moving undisturbed through their habitat.

(i.e., foraging), lizards move at very slow speeds (23% of maximal). These patterns are similar to those reported for other lizards (Irschick et al., 2005; Husak, 2006). In many instances, lizards that exhibit slower maximal speeds compensate by using a greater proportion of their maximal capacity in certain behavioral contexts (e.g., predator escape). Unfortunately, we were unable to test for locomotor compensation in the present study because animals proved very difficult to capture after video recording.

Animals may use primarily slow-speed locomotion when undisturbed and high-speed bursts during rare but important episodes (Irschick, 2000b). Overall, the ranges of speeds employed and distances moved in nature are rarely examined. *Ameiva ameiva* moves through its habitat using a very narrow range of speeds, which is suggestive of a preferred speed (Pennycuik, 1975; Hoyt and Taylor, 1981; Perry et al., 1988; Irschick, 2000b). Unlike some desert lizards (*Uma*), but similar to *Anolis*, *Ameiva* exhibit a unimodal distribution of undisturbed

locomotor speed (Irschick, 2000a,b). Thus, despite essentially constant activity, *Ameiva* move through their habitat using short, slow movements. This may be a consequence of an actively foraging lifestyle in teiids, in which undisturbed movement appears to be associated primarily with foraging. These animals move short distances interrupted by short pauses to root and search for food. Interestingly, distances per movement tended to be lower than those of *Anolis* lizards (Irschick, 2000a).

Physiological performance has become a critical avenue through which we can gain a deeper understanding of the evolutionary consequences of morphological variation (Arnold, 1983). Extensions to the original “morphology–performance–fitness” paradigm for studying adaptation incorporate a behavioral filter through which performance might be related to fitness (Garland and Losos, 1994; Irschick and Garland, 2001). Therefore, a key component is to understand how organisms actually perform in nature (i.e., ecological performance). Activities that elicit a higher proportion of maximal performance might represent likely targets of selection (Husak, 2006). For actively foraging lizards (such as *A. ameiva*), natural selection likely acts more strongly on locomotor speed when evading a predator than while foraging because these lizards use nearly 90% of their maximal capacity during the former activity. Whether or not the target of selection is maximal or ecological, performance requires further studies tracking the survival of individual animals.

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