

THE EFFECTS OF MORPHOLOGY AND PERCH DIAMETER ON SPRINT PERFORMANCE OF *ANOLIS* LIZARDS

BY JONATHAN B. LOSOS AND BARRY SINERVO

*Museum of Vertebrate Zoology and Department of Zoology, University of
California, Berkeley, CA 94720, USA*

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Summary

We investigated the mechanistic basis for the observed correlation between leg length and perch size among West Indian *Anolis* lizards by testing the hypothesis that species use those perches upon which they can move most effectively. We used four *Anolis* species which differed in leg length and perch use in nature. We measured maximum sprint speed on rods of several sizes. Longer-legged species ran faster on thick rods. The speed of all species declined on thinner rods, but long-legged species were affected to a greater extent in that all species ran at approximately the same speed on the smallest rod. The short-legged *A. valencienni* experienced much less difficulty moving on thin rods than did the other species. Variation in leg length among *Anolis* might thus represent an evolutionary trade-off between maximizing sprint speed and maximizing stability on thin perches.

Introduction

The comparative method, long a central tenet of evolutionary biology, interprets among-species correlations between morphology and ecology as evidence for adaptation (Darwin, 1859). The ecological importance of major morphological differences (e.g. flippers and legs) are obvious; recent studies of closely related taxa within a community have documented more subtle patterns of ecomorphological correlation and attempted to determine their causal basis. In some cases, the functional significance of morphological variation has been determined. For example, in many seed-eating birds, bill morphology affects which seeds can be utilized most efficiently, and species tend to use those seeds which they can handle most efficiently (e.g. Grant, 1986; Benkman, 1987; for an intraspecific example, see Smith, 1987). In many cases, however, the basis for ecomorphological relationships is less evident.

Among lizards, variation in limb length and aspects of behavior and ecology are often correlated. In the deserts of western Australia, for example, long-legged skinks of the genus *Ctenotus* tend to utilize open spaces, while shorter-legged congeners move within the dense vegetation (Pianka, 1969). Despite considerable

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research on lizard ecomorphology, no study has yet established a relationship between relative leg length and locomotor performance (Garland, 1985), much less demonstrated how morphology, performance capability, and ecology interact to establish ecomorphological patterns.

The ecology of lizards of the genus *Anolis* is, perhaps, better studied than that of any other lizard genus. Among anoles, a striking radiation has occurred independently on three (and perhaps all four) large islands in the Greater Antilles (Williams, 1972, 1983). Within an island, species have differentiated in morphology, behavior and ecology. Among islands, morphologically convergent species exhibit similar behavior and ecology (and belong to the same 'ecomorph' category, Williams, 1972). In particular, relative hind limb length and perch diameter are directly related; species similar in limb length tend to use perches of similar diameter (Williams, 1972, 1983; J. B. Losos, in preparation).

Biomechanical models predict that relatively long-legged animals should have correspondingly greater strides and hence run more rapidly, all else being equal (Hildebrand, 1974; Coombs, 1978). On thin perches (relative to body size), however, locomotor performance may be impaired because the legs are placed directly beneath the body and, consequently, are less effective at maintaining stability and preventing toppling. On such perches, shorter legs should be advantageous, because they lessen the distance between the center of mass and the surface, and hence minimize sideways torque (Cartmill, 1985; Pounds, 1988). In this study, we examine these models by testing the hypothesis that species use those perches on which they can move most effectively.

Species tested

We used four species of *Anolis* that attain approximately the same size (Table 1). *Anolis gundlachi* and *A. lineatopus* are 'trunk-ground' ecomorphs. They have very long hind legs and commonly perch on trunks, near the base of

Table 1. *Morphological and ecological measurements*

Species	Snout-vent length (mm)	Leg length (mm)	Leg/svl	Perch diameter (cm)
<i>Anolis gundlachi</i>	65.1 + 0.49	57.6 + 0.45	0.89	33.5 + 5.35
<i>A. lineatopus</i>	57.2 + 0.51	46.1 + 0.40	0.81	26.0 + 4.78
<i>A. grahami</i>	61.6 + 0.93	45.6 + 0.80	0.74	17.7 + 3.94
<i>A. valencienni</i>	72.1 + 1.69	38.5 + 0.76	0.53	6.0 + 2.01

All values are + 1 s.e.

Morphological measurements are from >20 adult males captured in the field.

Hind leg length is the distance on the outstretched leg from the distal tip of the fourth toe to the point of insertion in the body wall (Pianka, 1969).

Perch diameter is the mean size of the perch on which individuals (>30 per species) were first observed.

All data from J. B. Losos (in preparation).

svl, snout-vent length.

moderate-to-large trees [for more extensive discussion of the behavior and ecology of these species, see Rand (1964, 1967), Schoener & Schoener (1971*a,b*) and Hicks & Trivers (1983)]. They tend to use large-diameter substrates, often moving from the trunk to the ground (Williams, 1972; Moermond, 1979*a,b*; J. B. Losos, unpublished observations). *Anolis grahami*, a 'trunk-crown' ecomorph, has moderately long hind limbs. It also is seen on tree trunks, but usually is found higher in trees (Schoener & Schoener, 1971*a*; J. B. Losos, unpublished observations) and tends to move onto thinner, outlying branches. Those differences are reflected in the mean perch size used by these species (Table 1). *Anolis valencienni*, a 'twig' ecomorph, has extremely short legs, commonly utilizes thin twigs (Table 1), and actively searches for its prey, in contrast to most other anoles (Hicks & Trivers, 1983).

Materials and methods

Adult male lizards were collected in Jamaica (*A. lineatopus* Gray and *A. grahami* Gray: Discovery Bay, St Ann Parish; *A. valencienni* Duméril & Bibron: Southfield, St Elizabeth Parish) and Puerto Rico (*A. gundlachi* Peters: near El Verde, Luquillo Mtns) and transported to Berkeley, California, where they were maintained in 1.0 m × 1.0 m × 0.7 m cages (about 10 lizards per cage; no more than three lizards per species per cage) in a heated greenhouse with food and water provided *ad libitum*. Only healthy lizards (based on appearance and demeanor) were used in sprint trials.

We used maximum sprint speed as our measure of locomotor performance. Sprint speed has obvious ecological importance and can be reliably measured with high repeatability (Bennett, 1980; Garland, 1985; Huey & Dunham, 1987). Further, the biomechanical models outlined above predict that morphology and perch diameter interactively affect sprint speed.

We measured sprint speed on rods (artificial branches), covered with fiberglass window screening (1 mm mesh) to provide good traction, of the following diameters (cm): 1.2, 2.1, 2.6, 3.3, 4.6. Maximum sprint speed was measured by chasing a lizard up a rod angled at 45° (protocol modified from Huey, 1983; Garland, 1985; van Berkum, 1986). As the lizard ran up the track, it interrupted light beams stationed at 0.1 m intervals. A Compaq portable computer connected to the transistor photocells calculated the speed for each interval. The speed in the fastest of the 10 intervals was recorded for each run. Trials in which the lizard ran at sub-maximal speed (recognized by running posture and gait) were excluded. Lizards which jumped off the rod were re-tested immediately. Trials in which the lizard had obvious difficulty moving (e.g. losing balance, falling, running awkwardly or jumping off the rod) were noted. Lizards were run on each rod once per day, at hourly intervals. The order in which the rods were used each day was randomized. Four sets of trials were conducted with at least 1 day between consecutive trials. Lizards were warmed to 30°C (the optimal performance temperature for these species (Huey & Webster, 1976; Huey, 1983; van Berkum, 1986; R. B. Huey, personal communication) prior to each trial. For each lizard,

the fastest interval on a rod was considered the maximum sprint speed for that rod size. Some lizards produced no acceptable trials on some rod sizes, particularly the 1.2 cm rod.

Results

On the two largest rod sizes, there was a perfect rank correlation between hind limb length and sprint speed among species (Fig. 1). On the smaller rods, however, sprint speeds converged and they were indistinguishable on the smallest rod. Comparing the scores of individuals on smaller rods relative to the largest rod indicated that sensitivity of sprint speed to perch diameter (i.e. relative decrease in sprint speed on smaller rods) and leg length were perfectly rank-correlated (Table 2). Analysis of covariance on the sprint speed data (using species as a factor and rod size as a covariate) confirms this trend: the slope describing the decline in sprint speed as a function of rod size was greatest for the long-legged *A. gundlachi* and least for the short-legged *A. valencienni* (analysis using each individual separately: $F_{3,115} = 4.20$, $P < 0.01$; using mean values for each species on each rod size: $F_{3,12} = 8.01$, $P < 0.005$).

For each lizard, the number of trials in which it had difficulty running was compared for the 1.2 and 4.6 cm rods. Several lizards were excluded because we did not have data for all four trials on each rod. Only one lizard (an *A. valencienni*) had more trouble on the 4.6 cm rod. On the 4.6 cm rod, the species were again ordered by relative leg length, but the differences were not great (Table 3). By contrast, on the 1.2 cm rod, *A. gundlachi* had considerably greater, and *A. valencienni* considerably less, difficulty than the other two species. Each individual was assigned a differential difficulty index, i.e. the number of trials with

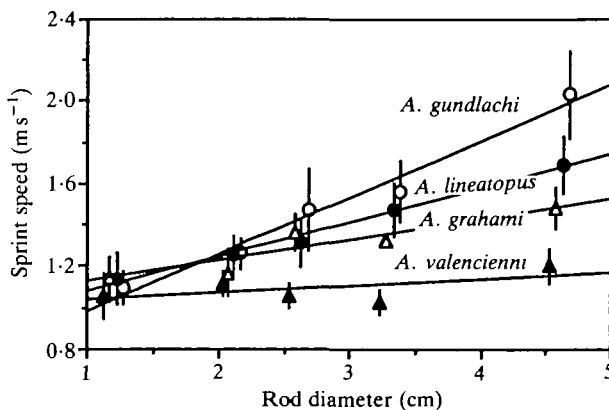


Fig. 1. Maximum sprint speed on rods of the following diameters: 1.2, 2.1, 2.6, 3.3 and 4.6 cm. Each point is the mean value for a species. Sample sizes are the same as in Table 2. Sample sizes for the 4.6 cm rod are: *Anolis gundlachi* (6), *A. lineatopus* (10), *A. grahami* (6) and *A. valencienni* (6). Points are offset for each rod diameter so that standard error bars will not overlap.

Table 2. *Sprint speed decrease on smaller branches*

Species	Sprint speed ratio			
	3.3/4.6	2.6/4.6	2.1/4.6	1.2/4.6
<i>Anolis gundlachi</i>	0.73 + 0.15 (5)	0.69 + 0.12 (5)	0.63 + 0.13 (5)	0.58 + 0.18 (3)
<i>A. lineatopus</i>	0.87 + 0.04 (10)	0.78 + 0.04 (10)	0.73 + 0.05 (9)	0.68 + 0.03 (10)
<i>A. grahami</i>	0.89 + 0.08 (6)	0.90 + 0.09 (5)	0.79 + 0.07 (5)	0.77 + 0.08 (4)
<i>A. valencienni</i>	0.89 + 0.05 (5)	0.94 + 0.09 (4)	0.94 + 0.05 (6)	0.87 + 0.20 (3)

For each individual, the ratio of its sprint speed on a branch relative to its speed on the 4.6 cm branch was calculated.

Values here are the mean for each species + 1 s.e.

Sample sizes are in parentheses.

Table 3. *Number of trials in which a lizard had difficulty*

Species	Rod diameter	
	4.6 cm	1.2 cm
<i>Anolis gundlachi</i>	0.67 + 0.23	3.17 + 0.34 (6)
<i>A. lineatopus</i>	0.50 + 0.29	1.75 + 0.48 (8)
<i>A. grahami</i>	0.50 + 0.25	1.83 + 0.52 (6)
<i>A. valencienni</i>	0.33 + 0.25	0.67 + 0.31 (9)

Values are the mean number (+ 1 s.e.) of trials out of four in which a lizard had difficulty running or jumped off.

Lizards that were not used in four trials on both branches are not included; lizards that ran at sub-maximal speeds or consistently jumped off are included.

Sample sizes are in parentheses.

difficulty on the 1.2 cm rod minus the number of trials with difficulty on the 4.6 cm rod. The index scores differed significantly among species, with the highest values for *A. gundlachi* and the lowest for *A. valencienni* (Kruskal-Wallis $H = 10.99$, 3 df., $P < 0.02$).

Discussion

Both biomechanical predictions are confirmed; sprint speed for all species declines on smaller perch sizes, but the sensitivity of sprint speed to perch diameter is lowest for short-legged species that more often utilize thin perches in nature. These species, however, neither exhibit maximum sprint performance nor

sprint faster than longer-legged species on thin perches (Fig. 1). It is clear why long-legged species like *A. gundlachi* and *A. lineatopus* almost never use thin perches (Rand, 1964, 1967; Schoener & Schoener, 1971a,b; J. B. Losos, personal observation), but even the twig specialist *A. valencienni* might run slightly faster on larger perches. In what way, then, are *A. valencienni*'s short legs and use of extremely thin perches, both evolutionarily derived features within the *Anolis* radiation (Underwood & Williams, 1959; Williams, 1983; J. B. Losos, in preparation) adaptive?

Sprint speed might not be the performance variable of greatest importance in determining the relationship between leg length and perch use. *Anolis valencienni* walks and crawls much more frequently than other anoles and hunts by methodically searching the substratum for cryptic prey, rather than by rapidly running and grabbing insects that pass nearby, as do other anoles (Hicks & Trivers, 1983; J. B. Losos, personal observation). Furthermore, *A. valencienni* slowly sidles around perches to avoid detection, although it will run to avoid capture (J. B. Losos, personal observation). Consequently, maximum sprint capability may be less important for *A. valencienni* than for other species.

Stability might be the performance parameter of greatest significance for species using thin perches. Our data indicate that *A. valencienni* has much less difficulty than longer-legged species in moving on thin perches. *Anolis gundlachi*, the species with longest legs and largest mean perch size in nature, averaged less than one trouble-free trial (out of four) per individual on the 1.2 cm branch. Anoles sometimes have difficulty moving, and even fall out of trees, in nature (Pounds, 1988; J. B. Losos, unpublished observation), but the interspecific relationship between leg length and locomotor difficulties in nature remains to be documented.

We suggest that variation in leg length among *Anolis* might thus represent an evolutionary trade-off between maximizing sprint speed and maximizing stability on thin perches. Species that utilize thin perches might have to alter their behavioral ecology in response to lessened sprinting and jumping capability [jumping ability is also proportional to leg length (Emerson, 1985; Pounds, 1988; J. B. Losos, in preparation)]. *Anolis valencienni*, atypical among anoles in its slow and continuous foraging mode, reliance on crypsis to avoid predation, and only weakly territorial social structure, might represent an extreme example.

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