WALKING THE TIGHT ROPE: ARBOREAL SPRINT PERFORMANCE AMONG SCELOROPUS OCCIDENTALIS LIZARD POPULATIONS

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Abstract. We document variation in the degree of arboreality among four populations of the western fence lizard (Sceloporus occidentalis), and investigate how this variation relates to locomotor performance capability in an arboreal context (e.g., artificial branches). We raced lizards on four different rod diameters, measured maximum sprint speed, and also scored agility on the rods. Lizards from more terrestrial populations ran faster on thick rods, but slower on thin rods than did lizards from more arboreal populations. The terrestrial lizards experienced a greater difference in sprint speed than did the more arboreal lizards over the range of rod sizes we used. Arboreal lizards were more adept at running on all surfaces in that they stumbled and fell less often, particularly from the thinnest rods. Thus, specialization for maximizing sprinting performance on arboreal surfaces of a particular diameter entails a performance trade-off that is reflected in both speed and “sure-footedness.” We investigated whether the population differences in arboreal sprinting are correlated with the significant differences in hind-limb span found among populations. We found that lizards with relatively longer limbs sprinted faster. By using juveniles reared in a common laboratory environment, we demonstrated that these among-population differences in arboreal sprint performance are probably genetically based.

Key words: agility vs. maximal performance; arboreal; ecomorphology; lizard; performance trade-off; Sceloporus occidentalis; sensitivity; sprint speed vs. perch diameter.

INTRODUCTION

Organismal performance has been implicated as a crucial link in our understanding of how natural selection might mold phenotype to the environment (Arnold 1983). The phenotype that produces optimal performance in one situation, however, is not necessarily the one that maximizes performance in other situations (Huey and Hertz 1984). Furthermore, organisms must be able to perform adequately in all situations they might experience in nature (Huey and Stevenson 1979). Consequently, organisms exposed to a variety of ecological situations might also be expected to have a wide performance breadth, i.e., the range of situations over which they perform adequately (Huey 1982). This hypothesis has been investigated in studies of the thermal sensitivity of sprint performance in lizards (Huey and Stevenson 1979, Hertz et al. 1983, Crowley 1985, John-Alder et al. 1986, van Berkum 1986, 1988). That is, species that experience a wider range of body temperatures in nature (broader ecological breadth) are expected to perform well over a greater range of temperatures than species that experience a narrow range of body temperatures (broader performance breadth).

The “ecological breadth–performance breadth” hypothesis (Huey and Stevenson 1979, Huey 1982) can be applied to other aspects of the environment. For example, species (Williams 1983) and populations

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MATERIALS AND METHODS

Study animals, study sites, and field observations

We obtained hatchlings from clutches of eggs laid by gravid females taken from our study populations during May and June 1988. Females from Washington were collected near Lyle (elevation: 200 m), Klickitat County; females from Oregon were collected near Terrebonne (750 m), Deschutes county; females from high elevation in California from the east side of Table Mountain (2230 m, Los Angeles County) near Wrightwood; and females from low elevation in California from the edge of the Mojave desert (1330 m), near Pearblossom, Los Angeles County.

All sites have abundant perches and openings in the trees for sun during most of the day, but the dominant landscape varies considerably [Washington: oak trees (Quercus sp.), logs, and open space; Oregon: juniper trees and logs (Juniperus sp.), sage (Artemisia sp.), rocks, and open space; California high elevation: predominately Jeffrey pine trees (Pinus jeffreyi), oak trees (Quercus kelloggi), and sage (Artemisia sp.), logs, stumps, rocks, and open space; California low elevation: Joshua trees and logs (arborescent Yucca brevifolia), juniper (Juniperus sp.), sage (Artemisia sp.), rocks, and open space]. Habitat structure was quantified following Adolph (1990a).

To quantify differences in microhabitat use among populations in nature, we noted the height at which each lizard was initially observed (0, 0–0.4, 0.4–0.8, 0.8–1, 1–2, and >2 m) and the orientation of the surface upon which it was perched (e.g., vertical: trees and branches; horizontal: logs, rocks, and stumps). Because we only used juvenile lizards in our laboratory measurements of sprint speed, we only include perch data from juveniles observed in nature. The Washington site was logged before quantitative perch data could be collected, but J. Tsiu (personal communication) has provided qualitative observations indicating that Washington lizards are very similar to Oregon lizards in their use of the habitat. All observations were made during the late summer and fall (1984–1987), when habitat use of juveniles was not likely to be influenced by the presence of adult lizards, which are less active and not reproductive during this season.

Juvenile rearing

Details of egg incubation and hatching rearing are found in Sinervo (1990). Juvenile lizards were provided crickets (dusted with calcium and vitamins: Nektos-N [Nektos-Produkte, Pforzheim, Germany]) and water ad libitum. Ultraviolet light bulbs provided background illumination. Individual hatchlings were initially maintained in small terraria (10 × 20 × 15 cm) with an incandescent light bulb placed over the corner to provide a thermal gradient for behavioral thermoregulation (Sinervo and Adolph 1989). After 6–7 wk, they were housed in groups of 3–12 (depending on size of the juveniles) in much larger plastic terraria (14 L) with wire-screen tops. By rearing hatchlings in a common laboratory environment we minimized potential environmentally induced (non-genetic) differences in sprint performance among populations arising from incubation temperature differences among populations, the effects of learning, or experience during ontogeny.

Animals were raced at 15–17 wk of age. Owing to differences in hatching date and growth rate, body sizes varied for each population (Washington: 2.9–6.3 g, Oregon: 1.9–5.3 g, high-elevation California: 1.4–7.0 g, and low-elevation California: 1.7–8.5 g). We measured mass before and after racing; all lizards grew during this 2-wk interval. At the end of the race trials, we measured snout–vent length (SVL), hind-limb span (HLS: distance from the fourth toe on each hind leg with the hind legs stretched out laterally), and thigh length (TL: distance from knee to knee with the femurs held orthogonal to the body axis [Garland, 1985]).

Performance measurements

Maximum sprint speed has obvious ecological importance and can be measured with high repeatability (Bennett 1980, Huey and Dunham 1987, van Berkum et al. 1989). We measured sprint speed (protocol modified from Huey 1983, Garland 1985, van Berkum et al. 1989) on 2.1, 2.6, 3.3, and 4.6 cm diameter rods (artificial branches made from PVC pipe). We took advantage of S. occidentalis’ propensity to escape vertically (B. Sinervo, personal observation) by chasing a lizard up a rod angled at 45°. The rod was covered with fiberglass window screening (1-mm mesh), which provided good traction.

Lizards were placed in a constant temperature incubator (34°C, the optimal temperature for sprinting in this species [Adolph 1987]) at least 1 h before racing began and between all subsequent races. As the lizard ran up the 1.5-m track it interrupted light beams stationed at 0.1-m intervals along the first 1.0 m of the track. The time interval between light stations provided a measure of speed over a given interval. The fastest 0.2-m speed (i.e., over two consecutive intervals) was recorded for each run. It is important to note that only races in which the lizard performed well (i.e., did not run awkwardly or lose its balance) over the entire 0.2-m interval were used in the analyses of sprint performance described below (see Statistical analyses). Lizards that experienced obvious difficulty (e.g., ran awkwardly, lost balance and/or fell off the rod) were re-raced once within 1 h on that rod. For each lizard, the proportion of trials on each rod size in which the lizard experienced such difficulty was considered our measure of “sure-footedness.”

Lizards were run on the four different rods once per day, at hourly intervals. The order in which the rods were used each day was randomized (subject to the constraint that each rod was used as the starting rod
only once, as the second rod only once, etc.). Thus, lizards were raced on four separate days with at least 1 d between consecutive trials. Of the 120 lizards available for racing, 113 produced at least three good runs out of four trials on each of the four rods.

**Statistical analyses**

The degree of arboreality among populations as measured in the field was analyzed using contingency table analysis. Two-way contingency table analysis was used to compare populations for degree of arboreality (i.e., frequency of use of ground, horizontal arboreal surfaces, or vertical arboreal surfaces). For the lizards on arboreal surfaces (horizontal or vertical) we also tested for among-population differences in perch height category using three-way contingency table analysis (Fienberg 1970, Schoener 1970, Bishop et al. 1975).

The fastest three trials on each rod were used in all subsequent analyses (i.e., at most we excluded only one trial per rod, the slowest trial). The 12 trials for each lizard represent 3 trials on each of four rods. We used repeated-measures analysis of covariance (SYSTAT: Wilkinson 1987) with two trial factors (race order to test for learning, and rod size) and source population used to group individuals (all data were ln-transformed). Because the speed of western fence lizard hatchlings is positively affected by body mass (van Berkum et al. 1989, Sinervo 1990), we adjusted all main effects using mass as a covariate. In these populations comparisons mass is preferable to SVL as a size covariate because the populations differ in “stockiness”—northern lizards carry more mass per unit of body length than southern lizards (Sinervo et al. 1991). Thus, using SVL rather than mass would confound aspects of morphology in the ANCOVA.

We compared hind-limb span (HLS) among populations by ANCOVA using body mass as the covariate. We used residuals from this ANCOVA as a measure of relative HLS. These residuals also have the population differences in HLS removed. Thus, these HLS residuals reflect the relative difference in hind-limb span among individuals within the populations that we used. The residuals that describe “relative leg length” can be used in conjunction with an analysis of sprint performance on each rod (subsection above) to determine whether HLS contributes to differences in sprint performance within populations. That is, we used a repeated-measures ANCOVA using the average speed on each rod as a trial factor (repeats on the same rod were pooled as an average), source population as a factor, and body mass as a covariate (with interaction terms), as well as the additional covariate “relative leg length.”

An alternative measure of performance, surefootedness (described above: *Performance measurements*), was compared among populations using Kruskal-Wallis one-way analysis of variance for each rod size. Surefootedness was scored for three of the four race days; thus we have three observations for each rod size for each lizard.

**Results**

**Arboreality in nature**

Habitat structure among the sites was broadly similar—all sites have abundant off-ground perches (Fig. 1a). Nonetheless, lizards from the study populations differed significantly in their tendency to use horizontal and vertical surfaces (Table 1) and in their perch heights on both horizontal and vertical surfaces (Fig. 2). Oregon lizards were observed primarily (97%) on the ground or on broad flat surfaces very close to the ground. In contrast, California low-elevation lizards were observed primarily on vertical surfaces (61%) and perched considerably higher. Moreover, although California low-elevation lizards are quite arboreal, they are nevertheless found in a diverse range of arboreal and terrestrial situations (Table 1, Fig. 2). California high-elevation lizards were intermediate in perch height and use of horizontal surfaces.

The three-way contingency table analysis (Table 2) suggests that only a model including all pairwise interaction terms between the variables (population [A], surface orientation [B], and perch height [C]) fits the data well. The G value assesses how well the model fits the data—the better the correspondence, the lower the G value. Only model 8 gives a good fit (nonsignificant difference) to the data. This suggests all the pairwise interaction terms are significant because leaving them out gives poor fit. The significance of the interaction terms implies that: (1) the populations differ in perch height (A × B); (2) the populations differ in choice of vertical or horizontal surface (A × C); (3) high perches tend to be vertical and low perches tend to be horizontal (B × C); and (4) for a given perch, the populations do not differ in choice of vertical vs. horizontal surface (model 8: not significantly different, i.e., no three-way interaction, Table 2a).

The dramatic differences in perch use among populations (Fig. 2) do not simply reflect differences in

<table>
<thead>
<tr>
<th>Table 1. Variation in arboreality in natural populations (%) observed in each perch category.*</th>
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</thead>
<tbody>
<tr>
<td>Perch surface</td>
</tr>
<tr>
<td>----------------</td>
</tr>
<tr>
<td>Vertical (e.g., tree, bush branches)</td>
</tr>
<tr>
<td>Horizontal (e.g., log, rock, stump)</td>
</tr>
<tr>
<td>Ground</td>
</tr>
</tbody>
</table>

*Heterogeneity among populations is significant (G = 130.71, df = 4, P < .001) as are all pairwise comparisons of populations (California [CA] low elevation vs. CA high elevation: G = 47.37, df = 2, P < .01; CA low vs. Oregon [OR]: G = 104.59, df = 2, P < .01; and CA high vs. OR: G = 21.49, df = 2, P < .01).
perch availability (Fig. 1a). Electivity indices (Fig. 1b), which correct for differences in habitat structure among sites (see legend of Fig. 1b for details of calculation), indicate that lizards at low elevation in southern California choose arboreal perches with a frequency greater than the availability of the perches would suggest. In contrast, Oregon lizards choose very low perches with a greater frequency than their availability. Lizards at high elevation in California are intermediate in this regard.

Sprint performance on different surfaces

Lizards sprinted significantly more slowly on thin rods than on thick ones regardless of source population (Fig. 3, Table 3, \( P < .001 \)). Moreover, the populations did differ significantly in sensitivity of sprint performance to rod diameter (repeated measures ANCOVA, Table 3, \( P < .001 \))—those populations that were more arboreal were less affected by decreasing rod diameter than those that were less arboreal (Fig. 3a). More interestingly, we observed a change in the rank order of sprint performance among populations on the extreme rod diameters. Although lizards from populations tending to be more arboreal in nature (e.g., California, Fig. 1) sprinted faster than the more terrestrial populations on thinner rods, lizards from more arboreal populations sprinted more slowly than the terrestrial populations on the largest rod diameter! Thus, the locomotor performance of lizards from the more arboreal populations was less sensitive to the effects of surface diameter in that they experienced a relatively smaller decrement in sprint speed with decreasing rod diameter (Fig. 3a). Moreover, the populations that were more arboreal in nature also had very few problems with any of the rods (i.e., they were more surefooted) in striking contrast to the difficulty experienced by the more-terrestrial populations (Fig. 3b).

Individuals did not show a training effect on the rods (i.e., the effect of trial number or race order on sprint speed was not significant; Table 3, \( P > .97 \)), but the interaction between trial number and population was significant (Table 3, \( P < .04 \)). This result may be biologically meaningless; inspection of the data revealed no consistent trend within any population for increased or decreased speed with training (data not shown; speed in the two northern populations went down then up with trial number and in the two southern populations went up then down). The multivariate polynomial repeated-measure tests (Winer 1971) indicated the linear term was not significant \( (P > .75) \), but the quadratic
term was \( P < .001 \). This reflects the difference in response among populations described above.

There were consistent differences in sprint performance among individuals. That is, significant variation in sprint performance was attributable to differences in the performance of individuals when tested on the same rod \( F_{108,216} = 8.16, P < .0001 \), reliability = 0.88) or when tested on different rods \( F_{108,324} = 10.83, P < .0001 \), reliability = 0.91) (Winer 1971).

Southern populations (California high and low) have relatively longer legs (ANCOVA, Fig. 4) than northern populations (Oregon and Washington; true also for adults, see Sinervo et al. 1991). Across the perch surfaces we used there was no association between relative leg length and overall sprint performance among populations. However, the sprint performance of longer-legged populations was less sensitive to the effects of perch diameter. We investigated the within-population relationship between relative leg length and sprint performance by correlating residual hind-limb span (HLS) with sprint speed (with population differences in HLS removed, see Statistical Analyses). Relative leg length had a significant effect on overall sprint speed when individuals from all populations were pooled (repeated-measures ANCOVA: effect of relative leg length: \( F_{1,107} = 5.641, P < .02 \). \( P \) values for other factors and covariates comparable to Table 3). The regression slope associated with the relationship between relative leg length and sprint performance is 0.66 \( (R = 0.16, \) based on residuals from ln-transformed data). Individual variation in relative leg length within populations had no effect on the sensitivity of sprint speed to surface diameter \( (P < .33) \).

**DISCUSSION**

**Performance trade-offs on different surfaces**

Our study has two clear results: (i) reduced perch diameter decreased sprinting ability in all the populations studied, and (ii) *S. occidentalis* from different populations varied both in the magnitude of the decrement in sprint speed as a function of decreased rod diameter and in their ability to negotiate rods successfully (Fig. 3b, Table 3). Lizards from the more terrestrial populations (Oregon and Washington) sprinted faster than the more arboreal populations (California) on the broad surfaces, but the terrestrial lizards sprinted more slowly than the more arboreal populations on the thinnest rods. Thus, the sprint performance of the more terrestrial lizards was more sensitive to rod diameter in that they experienced a greater decrement in sprint performance with decreased rod diameter. Although arboreal lizards did not run uniformly the fastest on all rods, they had a more consistent sprint performance across a variety of surfaces. Moreover, the lizards from more arboreal populations were more surefooted on all rods, particularly the
Table 2. Comparisons of populations (A) for differences in perch height (B) and surface orientation (C—horizontal or vertical). (a) Three-way contingency table analysis presenting the $G$ statistic for all possible models testing for association (interaction terms A $\times$ B, A $\times$ C, etc.) between the members of each pair of variables. (b) An alternative way to assess significance of an interaction is to compare the $G$ value of a model that contains a term with the $G$ value of a related model that lacks it (Fienberg 1970, Schoener 1970, Bishop et al. 1975).

(a) Contingency table analysis

<table>
<thead>
<tr>
<th>Model</th>
<th>$G$</th>
<th>df</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) A, B, C</td>
<td>343.73</td>
<td>22</td>
<td>$P &lt; .001$</td>
</tr>
<tr>
<td>(2) A, B, C, A $\times$ B</td>
<td>153.27</td>
<td>14</td>
<td>$P &lt; .001$</td>
</tr>
<tr>
<td>(3) A, B, C, A $\times$ C</td>
<td>225.51</td>
<td>20</td>
<td>$P &lt; .001$</td>
</tr>
<tr>
<td>(4) A, B, C, B $\times$ C</td>
<td>277.75</td>
<td>18</td>
<td>$P &lt; .001$</td>
</tr>
<tr>
<td>(5) A, B, C, A $\times$ B, A $\times$ C</td>
<td>35.05</td>
<td>12</td>
<td>$P &lt; .001$</td>
</tr>
<tr>
<td>(6) A, B, C, A $\times$ B, B $\times$ C</td>
<td>87.29</td>
<td>10</td>
<td>$P &lt; .001$</td>
</tr>
<tr>
<td>(7) A, B, C, A $\times$ C, B $\times$ C</td>
<td>139.53</td>
<td>16</td>
<td>$P &lt; .001$</td>
</tr>
<tr>
<td>(8) A, B, C, A $\times$ B, A $\times$ C, B $\times$ C</td>
<td>11.54</td>
<td>8</td>
<td>.1 $&lt; P &lt; .5$</td>
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</table>

(b) Comparison of models

<table>
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<tr>
<th>Term</th>
<th>$G$</th>
<th>df</th>
<th>Models</th>
<th>Significance</th>
</tr>
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<tbody>
<tr>
<td>A $\times$ B</td>
<td>190.46</td>
<td>8</td>
<td>(1 vs. 2)</td>
<td>$P &lt; .001$</td>
</tr>
<tr>
<td>A $\times$ B</td>
<td>147.99</td>
<td>8</td>
<td>(7 vs. 8)</td>
<td>$P &lt; .001$</td>
</tr>
<tr>
<td>A $\times$ C</td>
<td>118.22</td>
<td>2</td>
<td>(1 vs. 3)</td>
<td>$P &lt; .001$</td>
</tr>
<tr>
<td>A $\times$ C</td>
<td>75.75</td>
<td>2</td>
<td>(6 vs. 8)</td>
<td>$P &lt; .001$</td>
</tr>
<tr>
<td>B $\times$ C</td>
<td>65.98</td>
<td>4</td>
<td>(1 vs. 4)</td>
<td>$P &lt; .001$</td>
</tr>
<tr>
<td>B $\times$ C</td>
<td>23.51</td>
<td>4</td>
<td>(5 vs. 8)</td>
<td>$P &lt; .001$</td>
</tr>
</tbody>
</table>

...smallest (Fig. 3b). Thus, sprinting on arboreal surfaces may entail a performance trade-off that is reflected in both speed and surefootedness. Relatively high sprint speed and surefootedness on small diameter surfaces may not be possible without a decreased speed on larger surfaces.

Performance in an ecological context

These trade-offs are readily explicable in the context of the ecological setting of these populations. The populations are found in environments with similar habitat structure and complexity (Adolph 1990a; B. Sinervo, personal observation), but ground temperatures at midday force California lizards to be considerably more arboreal to maintain sublethal body temperatures (Adolph 1990a). In contrast, Washington lizards are found in an environment that permits the utilization of the ground or perches very close to the ground throughout most of the day (Tsui 1988). Consequently, lizards from Washington and Oregon spend most of their time on broad, flat, low surfaces, whereas lizards from California commonly utilize a broad spectrum of surface diameters ranging from the ground to small Joshua tree spines and high branches. In this context, Washington and Oregon lizards appear to have been able to specialize for locomotion on flat perches. In contrast, California lizards sprint well and are sure-footed (Fig. 3) on a variety of surfaces, and have sacrificed absolute maximal sprint speed for more consistent agility and speed over a range of surfaces.

Among-population differences in learning might confound the interpretation of genetic differentiation; animals taken from different study populations might differ because opportunity for practice on different sur-

Table 3. Repeated-measures analysis of covariance for sprint performance on rods. All main effects have been adjusted for the effect of the covariate (body mass). All data are ln-transformed. See Fig. 3a for sprint speed (adjusted cell means) in each population on rods of different sizes. * $P < .05$, *** $P < .001$.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>ss</th>
<th>df</th>
<th>ms</th>
<th>F</th>
<th>P</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Population (POP)</td>
<td>0.084</td>
<td>3</td>
<td>0.028</td>
<td>0.208</td>
<td>.891</td>
</tr>
<tr>
<td>Body mass (SIZE)</td>
<td>10.008</td>
<td>1</td>
<td>10.008</td>
<td>74.846</td>
<td>.000***</td>
</tr>
<tr>
<td>Subjects within groups</td>
<td>14.442</td>
<td>108</td>
<td>0.134</td>
<td></td>
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</tr>
<tr>
<td>Rod size (ROD)</td>
<td>0.211</td>
<td>3</td>
<td>0.070</td>
<td>5.692</td>
<td>.001***</td>
</tr>
<tr>
<td>ROD $\times$ POP</td>
<td>0.617</td>
<td>9</td>
<td>0.069</td>
<td>5.556</td>
<td>.000***</td>
</tr>
<tr>
<td>ROD $\times$ SIZE</td>
<td>0.088</td>
<td>3</td>
<td>0.029</td>
<td>2.338</td>
<td>.069</td>
</tr>
<tr>
<td>Residual</td>
<td>3.999</td>
<td>324</td>
<td>0.012</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trial number (TRIAL)</td>
<td>0.001</td>
<td>2</td>
<td>0.000</td>
<td>0.027</td>
<td>.973</td>
</tr>
<tr>
<td>TRIAL $\times$ POP</td>
<td>0.228</td>
<td>6</td>
<td>0.038</td>
<td>2.318</td>
<td>.034*</td>
</tr>
<tr>
<td>TRIAL $\times$ SIZE</td>
<td>0.002</td>
<td>2</td>
<td>0.001</td>
<td>0.061</td>
<td>.941</td>
</tr>
<tr>
<td>Residual</td>
<td>3.540</td>
<td>216</td>
<td>0.016</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
faces could amplify any innate differences arising from either microhabitat choice (Adolph 1990b) or performance capability (this study). However, the among-population differences in sprint sensitivity that we have documented reflect innate differences in abilities, because these juveniles were reared in a common laboratory environment and were not exposed to the confounding effects of different habitats. These innate differences in sprint sensitivity are likely to be genetically based because sprint performance of hatchling fence lizards has a heritable basis (Tsuji et al. 1989). Moreover, sprint performance of individual western fence lizards on arboreal surfaces is highly repeatable (Bennett 1980, Huey and Dunham 1987, van Berkum et al. 1989) on the same perch (reliability = 0.88) and across different perch sizes (reliability = 0.91).

It is a paradigm of evolutionary biology that specialization for one task leads to deficiencies in the performance of other tasks (e.g., “a jack of all trades is the master of none” [Huey and Hertz 1984]). This appears to be the case with locomotor performance in structurally diverse environments. Given the broader spectrum of sprinting surfaces in southern environments, differences in the sensitivity of sprinting ability to surface dimensions are perhaps the result of natural selection for generalist capability.

Results of our within-species comparison can perhaps elucidate the trends found in more extreme arboreal specialization in other lizards. For example, we have shown that a similar trade-off between sprint performance and agility on different surface diameters exists among Anolis lizards (Losos and Sinervo 1989). In particular, Anolis valencienni, which utilizes extremely thin branches, is insensitive to surface diameter and maintains good agility on small-diameter surfaces, but at the cost of much lower overall speed on broad surfaces. An extreme example of the trade-off of sprint performance and agility is provided by chameleons, which have evolved morphological structures and gaits to utilize narrow branches (Peterson 1984, Abu-Ghalyun et al. 1988) that necessarily preclude rapid sprint performance.

**Mechanistic basis of performance differences**

Our populations differ in hind-limb length (Fig. 4). Simple biomechanical models predict that longer-legged animals should be able to run faster, all else being equal (Sukhanov 1968, Hildebrand 1974, 1985, Garland 1985, Losos 1990). However, in different contexts, all else may not be equal, because movement on different surfaces may require changes in other parameters likely to affect sprint performance, including limb-cycling frequency, gait, posture, pelvic-girdle rotation, or vertebral flexure (Snyder 1954, Sukhanov 1968).

Our comparison among and within populations provided different answers concerning the effects of leg length on overall sprint performance and sprint sensitivity on different surfaces. These results are consistent with the idea that other important biomechanical parameters may vary among populations. Although the effect of leg length on overall sprint speed is evident within populations, the effects of leg length among populations may be masked by the magnitude of among-population changes in other parameters likely to affect performance. Similarly, the differences in sprint sensitivity and surefootedness, which are not a predicted consequence of variation in leg length, may result from among-population changes in other biomechanical pa-
habitats, or if performance is tested on the spectrum of situations encountered in nature.

In addition, further studies of performance capability in different contexts may provide a better understanding of the causal bases of habitat utilization. Recent biophysical studies have demonstrated how the thermal environment constrains which locations within the habitat can be utilized (Porter et al. 1973, Grant and Dunham 1988, Huey et al. 1989, Adolph 1990a).

Furthermore, within the subset of permissible locations, variation in the operative environmental temperature, and thus ectotherm body temperatures, can affect performance capability in nature (Christian and Tracy 1981, Waldschmidt and Tracy 1983, Snell et al. 1988). Similarly, the structural environment probably limits organisms to those parts of the habitat where they can perform adequately (see Performance in an ecological context, above), and thus locomotor performance capability as a function of habitat structure may contribute to the partitioning of the structural environment and resource use among species (Vitt et al. 1981). Indeed, the interaction between thermal and structural environments (Adolph 1990a) and their effects on performance may have been influential as a selective agent resulting in the among-population differences in arboreal sprinting found in S. occidentalis.

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**Literature Cited**


