A COMPARATIVE ANALYSIS OF THE ECOCOLOGICAL SIGNIFICANCE OF MAXIMAL LOCOMOTOR PERFORMANCE IN CARIBBEAN ANOLIS LIZARDS

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Abstract.—We examined the sprinting and jumping capabilities of eight West Indian Anolis species during three natural activities (escape from a predator, feeding, and undisturbed activity). We then compared these field data with maximal performance under optimal laboratory conditions to answer three questions: (1) Has maximal (i.e., laboratory) sprinting and jumping performance coevolved with field performance among species? (2) What proportion of their maximum capabilities do anoles sprint and jump in different ecological contexts? (3) Does a relationship exist between maximal sprinting and jumping ability and the proportion of maximal performance used in these contexts? Among species, maximal speed is tightly positively correlated with sprinting performance during both feeding and escape in the field. Sprinting speed during escape closely matches maximal sprinting ability (i.e., about 90% of maximum performance). By contrast, sprinting performance during undisturbed activity is markedly lower (about 32% of maximum) than maximal sprinting performance. Sprinting ability during feeding is intermediate (about 71% of maximum) between field escape and field undisturbed activity. In contrast to sprinting ability, jumping ability is always substantially less than maximum (about 40% of maximum during feeding and undisturbed activity). A negative relationship exists among species between maximal speed and the proportion to which species sprint to their maximal abilities during field escape.

Key words.—Adaptation, comparative, lizards, locomotion, phylogeny.

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The ability of organisms to perform specific ecological "tasks," such as capturing prey or escaping predators, may have far-reaching effects on organismal survival, reproduction, and growth (e.g., Arnold 1983; Pough 1989; Wainwright 1994). Because of the potential importance to fitness, studies of performance ability have been a cornerstone of evolutionary biology for over 30 years (see recent overviews in Pough 1989; Garland and Losos 1994). However, a critical assumption in such studies is that laboratory performance accurately reflects how organisms perform in nature (Hertz et al. 1988). Quantifying how organisms perform in nature is critical for elucidating the relationship between morphology, performance, and habitat use. If organisms do not use their maximal capabilities in nature, then selection cannot act upon maximal capabilities and their underlying phenotypic bases. In this case, performance ability would not be the intermediate "link" between morphology and fitness that it is envisioned to be (Arnold 1983).

In addition, understanding the ecological context in which organisms utilize their maximal capabilities is important for understanding why a trait evolved. For example, a positive correlation exists between limb length, laboratory sprint speed, and use of open areas in some Australian lizard species (reviewed in Garland and Losos 1994). Although these correlations suggest that longer legs have evolved adaptively in open habitats, perhaps as a result of the increased speed they confer, in the absence of field performance studies, determining why long legs and enhanced speed is advantageous is difficult. Only field performance studies can assess whether increased speed is actually utilized by these lizards. Although demonstrating that faster individuals have higher fitness within a population is informative (e.g., Bennett and Huey 1990; Jayne and Bennett 1990), these studies by themselves cannot reveal the underlying mechanism for enhanced fitness. It is possible that the ability to run quickly is important for capturing prey in one species, but is important for escaping predators in another species.

One method for understanding how maximal and field performance are related is to examine whether these two characteristics have coevolved among species. Interspecific comparisons allow one to look at evolutionary changes occurring over fairly long time periods. Because these evolutionary changes are likely to be much greater than differences among individuals within a species, interspecific comparisons will be more likely than intraspecific comparisons to detect whether evolutionary changes in field performance and maximal performance are related to one another. Therefore, we utilized this interspecific approach to examine several hypotheses regarding the relationship between field and maximal performance among Anolis lizard species.

We examine how the sprinting and jumping capabilities of eight West Indian Anolis lizard species are used during three natural activities (escape from a predator, feeding, and undisturbed activity). We then compare these field performance data with the maximal performance of each species as determined under optimal laboratory conditions. Previous studies have demonstrated that maximal sprinting ability in reptiles is heritable (van Berkum and Tsuii 1987; Garland et al. 1990; Garland 1994), repeatable (Huey and Dunham 1987), and in a few cases, important to fitness (Bennett and Huey 1990; Jayne and Bennett 1990). Although jumping ability has not received similar attention, previous work on anoles (Moermont 1979; Pounds 1988; Losos 1990a,b,c) suggests that the ability to jump well is important for locomotion in anoles.

We address three questions: (1) Has maximal sprinting and jumping performance coevolved with field performance among species? In other words, are good sprinters and jump-
ers in the laboratory also good performers in all ecological contexts? (2) What proportion of their maximum capabilities do anoles sprint and jump in different ecological contexts? (3) Does a relationship exist between maximal sprinting and jumping ability and the extent to which these abilities are used?

**Background on West Indian Anolis Lizards**

West Indian Anolis lizards are an attractive group for examining questions concerning locomotor performance. On each of the Greater Antillean Islands of Cuba, Hispaniola, Puerto Rico, and Jamaica, anoles have undergone largely independent radiations, resulting in a series of ecologically and morphologically distinct types, termed “ecomorphs” (Rand and Williams 1969; Williams 1972, 1983; Losos 1990a; Jackman et al. 1998a). These ecomorphs differ in body shape characteristics (e.g., limb dimensions, toepad size, relative body mass, and tail length) that are correlated with differences in structural habitat use (Losos 1990a; Glossip and Losos, in press). These differences in morphology and habitat use are correlated with differences in behavior and locomotor performance (Moermond 1979; Losos and Sinervo 1989; Losos 1990a,b,c; Losos and Irschick 1996). For example, longer-limbed, stocky anole species tend to be good runners and jumpers in the laboratory, and also run and jump often in nature. By contrast, shorter-limbed, more slender anole species are poor runners and jumpers in the laboratory, and tend to walk more frequently in nature.

These studies suggest that the ability to sprint quickly and jump far is more important for some anole ecomorphs than others, but do not reveal in which ecological contexts sprinting or jumping is important. We gathered data on eight Anolis species representing three ecomorphs (three trunk-ground, three trunk-crown, and two twig anoles). These three ecomorphs differ ecologically and morphologically (for more details, see Losos 1990a). Trunk-ground anoles are stocky, have long tails and long hindlimbs, and use broad surfaces (e.g., tree trunks) close to the ground (usually <2 m). On the other extreme, twig anoles are slender, have short limbs and tails, use narrow surfaces (e.g., twigs), and occur relatively high (>2 m) off the ground. Trunk-crown anoles tend to be intermediate between these two ecomorphs in these characteristics.

Because evolution in Greater Antillean anoles has consisted primarily of divergence within islands and convergence between islands (Williams 1972, 1983; Losos 1990a, 1995; Jackman et al. 1998a), we sampled anole species that have evolved independently on three islands (Jamaica, Puerto Rico, and Cuba) so that members of an ecomorph class that we examined were not closely related.

**Methods**

**Laboratory Performance Trials**

We sampled a total of eight anole species, four of which were sampled as part of this study. Maximal sprinting data for two anole species (A. valenciennii and A. grahami) were taken from Losos and Sinervo (1989) and data for two other anoles (A. sagrei and A. carolinensis) were taken from Losos and Irschick (1996). Because conditions used in Losos and Sinervo (1989) differ slightly from those used in Losos and Irschick (1996) and this paper, we compared whether the maximal sprinting capabilities of a species (A. lineatopus) used in Losos and Sinervo (1989) and this study were similar. Both the mean values and the ranges of maximal speed were almost identical (Losos and Sinervo: mean = 1.7 m/s ± 0.20 [SE], max. = 2.3 m/s, min. = 1.2 m/s; this study: mean = 1.7 m/s ± 0.22, max. = 2.3 m/s, min. = 1.3 m/s). Given this close correspondence, we consider slight differences in laboratory conditions to be inconsequential. Maximal jumping data for all anole species except A. carolinensis (data from Losos and Irschick 1996) were from Losos (1990a); details of how data were collected are in that paper. No maximal jumping data were available for A. angusticeps.

Lizards were collected by hand or by using a slip-noose attached to a fishing pole a day prior to performance trials. Only healthy lizards (i.e., none with shrunken tail bases) were used in performance trials. Lizards were later released at the original site of capture. With the exception of maximal performance data taken from Losos (1990a), Losos and Irschick (1996), and Losos and Sinervo (1989), all maximal performance trials were carried out in field stations (Discovery Bay Marine Laboratory, Jamaica), or in housing units adjacent to sites where field data were collected (Puerto Rico). Performance data were gathered only on field-fresh lizards (i.e., lizards captured within 1–2 d) during the same time frame (i.e., within 1–2 mo) in which field data were collected.

Previous studies of maximal sprinting capabilities in anoles have demonstrated that anoles perform best (i.e., optimal performance) at temperatures close to their preferred temperature (Huey 1983; van Berkum 1986). All performance trials took place between 28–30°C. This temperature range corresponds roughly to air temperatures at perch sites used by anole species in this study, although body temperatures in some species may be slightly higher than air temperatures (see also Huey and Webster 1976; Hertz 1981, 1992).

Maximal sprinting ability was measured on a two-meter racetrack. The track surface was a 5.1-cm-wide dowel covered with fiberglass window screening (1.6-mm mesh) to provide good traction. Plexiglas boards were placed on both sides of the track to prevent lizards from jumping off the platform. Infrared emitters and receptors positioned every 25 cm were triggered by lizards sprinting along the dowel. These sensors were connected to a laptop computer that calculated speed over each interval. A cloth was draped over the end of the racetrack to provide a refuge toward which lizards ran.

Because Anolis lizards hop on horizontal surfaces, the race-track was angled upward at 37° to match experimental conditions in Losos and Irschick (1996). For each trial, lizards were positioned at the beginning of the dowel and induced to run by repeated taps to the tail. Each run was given either a “good” or “poor” rating; lizards that cycled limbs rapidly were given a good rating, whereas lizards that moved their limbs only partially and exerted suboptimal effort were given a poor rating. Only speeds from good runs were used in subsequent analyses. The greatest speed over a 25-cm interval was considered the estimate of maximal sprinting ability for each lizard.

We consider sprinting and jumping performance under
these laboratory conditions to approximate the maximal speeds and jumps of which *Anolis* lizards are capable. Maximal sprinting ability decreases in anoles due to decreased support diameter and smooth surface texture (Losos and Sinervo 1989; Losos and Irschick 1996; Irschick, unpubl. data). Maximal sprinting ability is independent of slope in small lizards (Huey and Hertz 1982). Hence, broad surfaces with rough texture should promote maximal sprinting performance. By contrast, maximal jumping performance is only slightly affected by these variables (Losos and Irschick 1996).

**Field Performance Trials**

Field data were collected in habitat surrounding Discovery Bay Marine Laboratory (Jamaica; *A. grahami*, *A. lineatopus*, *A. valenciennii*), Luquillo National Forest (Puerto Rico; *A. gundlachi*, *A. evermanni*), South Bimini Island (Bahamas; *A. angusticeps*, *A. sagrei*), and Jean Lafitte State Park (Louisiana; *A. carolinensis*). Field performance data and body mass data were gathered from the same localities from which specimens used in maximal performance trials were collected. Field data were collected in Puerto Rico from the beginning of May until mid-June 1995, in Jamaica from May to mid-June 1996, in the Bahamas from July 8–28, 1996, and in Louisiana from September 8–15, 1996.

During field trials, one person operated the video camera while another person acted as either the predator (escape trials) or operated the fly rod (feeding trials). For feeding trials, we used an artificial fly (resembling a mosquito, an insect eaten by anoles [Irschick, pers. obs.]) attached by line to the end of a two-meter pole. The fly was placed on a substrate approximately one meter away from each lizard. Almost all lizards chased the fly energetically and tried to eat it. For the escape trials, lizards were approached at a constant pace (approximately 30 m/min) until they fled. For this study, we equate fleeing behavior with escape behavior. Finally, to examine locomotor performance when moving undisturbed, we quietly observed lizards for periods ranging from 5–35 minutes. Any lizard disturbed prior to being detected by the observer was excluded from analyses.

A Hi-8 SONY video camera was used to film all locomotion events. After each trial, videotapes were reviewed in the field to determine distances (recorded to the nearest cm) of all jumps and runs. Distances were measured by reference to landmarks on natural substrates. Videotapes were later reviewed using a Hi-8 SONY video recorder to determine duration of all runs, which was determined by counting the number of frames (30 frames/second) elapsed between the beginning and end of a movement. Speed was measured in m/s for each movement. Jumps that took place over a vertical distance greater than 28 cm (the standard laboratory vertical distance) were excluded from analyses to avoid inflation of field jump distances. A run or jump had to be at least five centimeters to be considered a movement. For each escape, feeding, and undisturbed activity trial, we chose the fastest speed within each trial (i.e., if a lizard made three movements to capture a fly, we used the fastest of the three movements) as our estimate of maximal performance for that lizard.

To ensure that differences among individuals in field performance were not related to differences in habitat use, we measured five structural habitat variables on each individual examined: perch height, perch diameter, and distance to the nearest perch in each of the following three size classes: 0.2–0.8 cm (*D*small), 0.9–1.5 cm (*D*medium) and > 1.5 cm (*D*large). These ecological variables were chosen because *Anolis* species tend to differ in them (Rand and Williams 1969; Schoener and Schoener 1971a,b; Pounds 1988; Losos and Irschick 1990a), and because some of them can potentially affect locomotor performance (Losos and Sinervo 1989; Losos and Irschick 1996). In addition, we also measured air temperature (shaded-bulb air temperature at point lizard was originally seen), perch type (e.g., tree trunk), substrate texture (e.g., smooth), and orientation (e.g., pointed up) of each lizard when first seen.

**Statistical Analyses**

All statistical analyses are two-tailed and were carried out using SYSTAT 5.03 (Wilkinson 1990). We examined relationships among both nontransformed and log10-transformed variables and found that transformation did not substantially affect either the magnitude or the direction of the correlations (correlation values always differed by less than 0.05). Consequently, we present results from only nontransformed comparisons. Most of our analyses involve comparing performance of a species at two activities (e.g., does *A. sagrei* run faster during escape than feeding?). Because this kind of comparison is between two activities within a single species, body size is not a confounding factor. Body mass was not significantly correlated with maximal speed within any species (Pearson correlation tests, all *P*-values > 0.05), probably because we examined only adult males, which varied relatively little in body mass intraspecifically.

Because both escape speed and feeding speed exhibit strong positive correlations with body mass across species (Pearson r-values between independent contrasts = 0.52 and 0.76, respectively), effects of body size were removed for across-species comparisons by regressing independent contrasts (see below) of each performance variable on independent contrasts of body mass and calculating residuals (with the exception of relationships between maximal performance and percent maximal performance in nature, for which non-size-adjusted values were used). In each case, we plotted residual values of each performance variable against body mass to ensure that body mass did not remain correlated with the performance variables; and in all cases, there was no significant relationship between variables (Pearson correlation tests among residual values, all *P*-values > 0.05). Because only four lizard species jumped during feeding, and no more than one or two lizards within each species jumped during escape, we decided that these sample sizes were insufficient to either have sufficient power for correlations (for feeding) or accurately estimate mean values (for escape).

As an index of how closely each anole species sprinted or jumped to their maximal capabilities, we divided the mean field performance value of each species by the corresponding mean maximal value (e.g., mean escape speed divided by mean maximal speed) and calculated percent maximal performance values for each species during each activity. We plotted out relationships between numerators and denomi-
Fig. 1. A phylogenetic tree for eight Anolis lizard species based primarily on studies of mitochondrial DNA sequences (Jackman et al. 1998b). (See this reference for branch lengths.) Locality headings next to species names represent the Caribbean islands on which these species now occur. JAM, Jamaica; PR, Puerto Rico; BAH, Bahamas.

Fig. 2. The tree shows that the Anolis species have evolved in the Caribbean islands from a common ancestor. The branch lengths represent the number of nucleotide substitutions per site.

Phylogenetic Analyses

Because species are related to one another in a hierarchical fashion, species cannot be considered statistically independent (e.g., Felsenstein 1985; Martins and Garland 1991; Garland et al. 1992). The independent contrasts method (Felsenstein 1985) has been demonstrated to be successful for analyzing quantitative data within a phylogenetic context (Martins and Garland 1991). This method requires a fully resolved tree as well as branch lengths for the species under study, and assumes that evolution of the characteristics under study follows a Brownian motion model (Felsenstein 1985). Mitochondrial DNA sequences of the CO1 and the five adjacent transfer RNAs (Jackman et al. 1998b) have been gathered for six of the eight species used in this study (all except the Puerto Rican species A. evermanni and A. gundlachi), and provide good support for the tree in Figure 1 (for more details, see Jackman et al., unpubl. data). However, although sequences for A. evermanni and A. gundlachi were not available, two Puerto Rican taxa closely related to these two species (A. cristatellus and A. stratus) were included in those studies. Previous studies based on protein allozyme and karyotypic data have shown that A. evermanni and A. stratus are sister taxa, and that A. cristatellus and A. gundlachi are very closely related (Gorman et al. 1983).

We calculated branch lengths (maximum-likelihood distances assuming a molecular clock) by placing A. stratus and A. cristatellus in the place of A. evermanni and A. gundlachi, respectively (Jackman et al. 1998b). Using these branch lengths assumes that the number of nucleotide substitutions increases linearly with time, and that evolutionary changes in performance are a linear function of time elapsed. We also conducted analyses in which branch lengths were set equal to each other. Because results of this analysis were similar to the previous analysis, we only present results from the former. Regression and correlation values were calculated as suggested by Felsenstein (1985). We looked for significant correlations between the standard deviations of branch lengths and absolute values of independent contrasts (e.g., Garland et al. 1992), and found that all contrasts were appropriately standardized (Pearson correlation values all < 0.60, P-values > 0.10).

RESULTS

None of the environmental variables (e.g., temperature, orientation) were significantly correlated with jumping ability or sprinting ability during any activity (Pearson correlation tests, P > 0.05 for all comparisons). Therefore, we did not adjust for any environmental effects on jumping and sprinting ability.

Sample sizes and mean sprinting and jumping data are provided in Tables 1 and 2, respectively. Both speed and jumping distance differed significantly (one-way ANOVAs, P < 0.001 for all comparisons) among different activities within each species. Correlation values are generally similar when effects of body size are removed or not, with the exception of the relationship between escape speed and feeding speed, which are significant in the comparisons that are not size-adjusted but become nonsignificant when body size effects are removed (Table 3). Among species, both escape speed and feeding speed are positively correlated with maximal speed, as well as with one another (Table 3). Maximal jumping ability is positively correlated with undisturbed speed (Table 3).

Among species, escape speed closely matches maximal speed (mean of all species = 90.6% ± 3.80 SE). Maximal abilities are used less during feeding (mean = 71.3% ± 6.22), and hardly at all during undisturbed activity (mean = 32.5% ± 5.07) (Fig. 2). On the other hand, jumping performance, both during feeding (mean = 34.5% ± 7.19) and undisturbed activity (mean = 43.9% ± 4.40), does not closely match maximal jumping performance (Fig. 2). A negative relationship exists among species between maximal speed and the proportion to which species perform maximally during escape (Fig. 3). Similar comparisons between maximal performance and proportions of maximal performance used in nature were nonsignificant (all r-values < 0.45, all P-values > 0.10).

DISCUSSION

Several findings arise from our analyses. (1) Among species, maximal speed has coevolved with sprinting ability dur-
TABLE 1. Mean (± 1 SE) values for body mass, maximal sprinting performance, and field sprinting performance for eight Anolis species. All performance variables are in m/s. Numbers in brackets are number of individuals sampled per species. TG, trunk-ground; TC, trunk-crown; TW, twig. Body mass data (g) were gathered on a minimum of 10 adult males from the same locality in which laboratory and field data were collected.

<table>
<thead>
<tr>
<th>Species</th>
<th>Body mass (g)</th>
<th>Maximal</th>
<th>Escape</th>
<th>Feeding</th>
<th>Undisturbed activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. sagrei</td>
<td>2.9 ± 0.09</td>
<td>1.8 ± 0.04</td>
<td>1.3 ± 0.08</td>
<td>1.1 ± 0.08</td>
<td>0.4 ± 0.08</td>
</tr>
<tr>
<td>TG</td>
<td></td>
<td>[17]</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>A. lineatopus</td>
<td>4.6 ± 0.51</td>
<td>1.7 ± 0.05</td>
<td>1.4 ± 0.12</td>
<td>0.9 ± 0.08</td>
<td>0.8 ± 0.12</td>
</tr>
<tr>
<td>TG</td>
<td></td>
<td>[19]</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. gundlachi</td>
<td>7.1 ± 0.18</td>
<td>1.4 ± 0.16</td>
<td>1.3 ± 0.08</td>
<td>1.1 ± 0.08</td>
<td>0.5 ± 0.05</td>
</tr>
<tr>
<td>TG</td>
<td></td>
<td>[18]</td>
<td></td>
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<td></td>
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<tr>
<td>A. carolinensis</td>
<td>6.0 ± 0.26</td>
<td>1.2 ± 0.03</td>
<td>1.1 ± 0.05</td>
<td>1.0 ± 0.07</td>
<td>0.2 ± 0.06</td>
</tr>
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<td>TC</td>
<td></td>
<td>[22]</td>
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<tr>
<td>A. grahami</td>
<td>6.2 ± 0.23</td>
<td>1.5 ± 0.12</td>
<td>1.3 ± 0.07</td>
<td>1.2 ± 0.07</td>
<td>0.5 ± 0.05</td>
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<td>TC</td>
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<td>[6]</td>
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<td></td>
<td></td>
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<td>A. evermanni</td>
<td>5.6 ± 0.28</td>
<td>1.2 ± 0.03</td>
<td>1.1 ± 0.08</td>
<td>1.1 ± 0.10</td>
<td>0.7 ± 0.11</td>
</tr>
<tr>
<td>TC</td>
<td></td>
<td>[17]</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>A. valencienni</td>
<td>6.8 ± 0.73</td>
<td>1.2 ± 0.07</td>
<td>1.3 ± 0.16</td>
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<td>0.2 ± 0.08</td>
</tr>
<tr>
<td>TW</td>
<td></td>
<td>[16]</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. angusticeps</td>
<td>2.0 ± 0.08</td>
<td>0.8 ± 0.10</td>
<td>0.8 ± 0.10</td>
<td>0.4 ± 0.12</td>
<td>0.3 ± 0.09</td>
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<td>TW</td>
<td></td>
<td>[10]</td>
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</table>

Evolutionary Implications

Arnold (1983) envisioned that performance ability was the crucial intermediate step between morphology and fitness. However, the assumption that organisms always perform to their maximal capabilities has rarely been tested (Hertz et al. 1988; Pough 1989). This assumption is critical for understanding how selection acts upon characteristics such as maximal sprinting ability. Our study demonstrates that the degree to which maximal sprinting and jumping abilities are used by anoles varies in different ecological contexts, which suggests that selection on performance abilities is more likely to occur in some ecological contexts than others. Anoles sprint very close to their maximal abilities during escape. Consequently, if the likelihood of escaping successfully is a function of speed, then selection may act on maximal capabilities and lead to evolutionary changes in phenotypic traits associated with sprint speed. By contrast, anoles generally sprint about 30% less than maximum when chasing prey. Laboratory studies on the lizard Psammodromus algirus

TABLE 2. Mean (± 1 SE) jumping distances (cm) for eight Anolis species. Not enough lizards jumped during escape to calculate mean values. Maximal data were taken from Losos (1990a) for all species except A. carolinensis, for which data were taken from Losos and Irshich (1996). Numbers in brackets are number of individuals sampled per species. See the above references for sample sizes for maximal data.

<table>
<thead>
<tr>
<th>Species</th>
<th>Maximal jumping</th>
<th>Feeding jumping</th>
<th>Undisturbed activity jumping</th>
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</thead>
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<tr>
<td>A. sagrei</td>
<td>61.6 ± 1.29</td>
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<td>24.7 ± 3.20</td>
</tr>
<tr>
<td>A. lineatopus</td>
<td>75.7 ± 2.53</td>
<td>14.0 ± 3.61</td>
<td>28.1 ± 4.21</td>
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<tr>
<td>A. gundlachi</td>
<td>81.4 ± 1.89</td>
<td>31.4 ± 3.39</td>
<td>40.6 ± 3.52</td>
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<tr>
<td>A. carolinensis</td>
<td>5.20 ± 2.50</td>
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<td>22.5 ± 7.50</td>
</tr>
<tr>
<td>A. grahami</td>
<td>74.3 ± 2.40</td>
<td>21.3 ± 4.33</td>
<td>19.0 ± 3.40</td>
</tr>
<tr>
<td>A. evermanni</td>
<td>67.0 ± 1.70</td>
<td>35.0 ± 4.79</td>
<td>42.1 ± 4.21</td>
</tr>
<tr>
<td>A. valencienni</td>
<td>56.6 ± 1.52</td>
<td>—</td>
<td>27.6 ± 6.12</td>
</tr>
<tr>
<td>A. angusticeps</td>
<td>—</td>
<td>—</td>
<td>16.7 ± 3.18</td>
</tr>
</tbody>
</table>

TABLE 3. Matrix of Pearson correlation coefficients among independent contrasts for maximal and field sprinting and jumping performance. Each comparison has six degrees of freedom, except comparisons among feeding speed, maximal jumping, and other variables, which have five degrees of freedom. The bottom left half of the matrix is for values that were not size adjusted, whereas the top right side is for size-adjusted values. Variables that exhibited no significant correlations with any other variables were not included. *, P < 0.05, **, P < 0.01, ***, P < 0.001.

<table>
<thead>
<tr>
<th></th>
<th>Max. speed</th>
<th>Escape speed</th>
<th>Feeding speed</th>
<th>Undis. act. speed</th>
<th>Max. jumping</th>
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<td>Maximal speed</td>
<td>—</td>
<td>0.95***</td>
<td>0.79*</td>
<td>0.47</td>
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<tr>
<td>Escape speed</td>
<td>0.86**</td>
<td>—</td>
<td>0.65</td>
<td>0.47</td>
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<tr>
<td>Feeding speed</td>
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<td>0.83*</td>
<td>—</td>
<td>0.18</td>
<td>0.10</td>
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<tr>
<td>Undisturbed activity speed</td>
<td>0.48</td>
<td>0.42</td>
<td>0.30</td>
<td>—</td>
<td>0.79*</td>
</tr>
<tr>
<td>Maximal jumping</td>
<td>0.42</td>
<td>0.53</td>
<td>0.28</td>
<td>0.76*</td>
<td>—</td>
</tr>
</tbody>
</table>
studies that directly link field performance with fitness would be ideal for understanding whether the intensity of selection on sprinting performance is proportional to the percent to which maximal abilities are used in different contexts. Studies are currently planned to test this possibility.

Unlike sprinting ability, jumping performance in anoles during any natural activity was always much less than their maximal capabilities. This result is probably not due to unfavorable field conditions, as maximal jumping ability is not greatly affected by perch diameter (Losos and Irshick 1996) or surface texture (Irshick, unpubl. data). If anoles jump to their maximal abilities infrequently in nature, why have such great abilities evolved? One possibility is that the ability to jump far is important for some natural activity that we did not examine here (e.g., conspecific social encounters). A more likely explanation is that maximal sprinting and jumping ability have coevolved among anole species because of their mechanistic link with hindlimb length (Losos 1990b). Selection for long hindlimbs to enable faster sprinting would also lead to enhanced maximal jumping ability in anoles. Thus, it is possible that anoles have evolved a performance capability (maximal jumping) that may be unimportant to fitness. This finding underscores the importance of conducting field and laboratory studies of performance in parallel to ensure that organisms actually perform in nature as they are forced to do in the laboratory (Pough 1989). For example, studies of selection on maximal jumping ability in anoles would probably be misguided.

Proximate Influences on Field Performance

At a more proximal level, what are some of the factors that influence why anoles move at different speeds during different activities? One possible reason for why speed differs during escape and feeding is that differences in the dynamics of escape and prey capture place constraints on how fast lizards can move during the two activities. During feeding, all anoles typically first spotted the prey item, made a single moderately long (about 30–40 cm) and quick movement to
within 10–35 cm of the fly, paused, and then quickly dashed to grab the fly. This feeding technique is not an artifact of the feeding setup used here, as lizards used the same feeding behavior when capturing natural prey (Moermond 1981). However, during escape, lizards typically made one long (> 50 cm) dash either up a tree or into underbrush (distances moved during field escape were greater than during feeding in each of the seven species examined for both variables, Wilcoxon signed-ranks test, Z = -2.37, P < 0.05). This habit of “pausing” in front of the fly may explain why anoles run slower during feeding than escape. Because lizards are forced to accelerate and decelerate over a fairly short distance during feeding, unlike escape, the overall speed during the first long run may be slower than if the lizard had ran as fast as possible for a longer distance. Laboratory studies of sprinting in the agamid lizard *Stellio stellio* (Huey and Hertz 1982) have shown that they typically reach top speeds (95% of maximum) within about 40 cm, which is the upper distance limit of single runs during feeding in anoles. Studies of acceleration in anoles would thus be helpful in understanding whether anoles can achieve top speed over short distances as well. An alternative hypothesis that might explain greater escape speeds is that to avoid predators, lizards may use escape routes with which they are familiar, and thus can run quickly on, whereas to capture prey, they must move over potentially unfamiliar terrain to get to the prey item, and thus must move more slowly (Stamps 1995).

The only significant correlation between maximal jumping performance and other variables was between maximal jumping ability and undisturbed activity speed. Anole species that move quickly when undisturbed tend to be good jumpers in the laboratory. This correlation exists in part because the two species that move the slowest during undisturbed activity (*A. carolinensis* and *A. valetieni*) are also the worst jumpers (excluding *A. angusticeps*, for which no maximal jumping data are available). The poor maximal jumping ability of these two species is mechanistically tied to their relatively short hindlimbs, an adaptation in lizard species that frequent narrow perches (Moermond 1979; Cartmill 1985; Pounds 1988, Losos 1990c). Short limbs and a slender body enable greater dexterity on narrow supports by keeping the center of gravity positioned over the support (Cartmill 1985). Both *A. carolinensis* and *A. valetieni* are slender and frequently use narrow perches in nature, relying more on stealth than speed to avoid being captured (Hicks and Trivers 1983). This above-mentioned correlation thus fits in with comparative analyses showing that the habits of crypticity, being slow-moving, and having short limbs, have coevolved in anoles (Losos 1990a,c; Irschick and Losos 1996).

**Relationships between Maximal Speed and Effort**

We found a negative correlation among species between maximal speed and proportion maximal speed used during field escape. In other words, faster anole species tend to use their maximal sprinting capabilities less than slower anole species. One possible explanation for this relationship is that faster anole species ran longer distances than slower anole species during escape, and that the longer escape distances had greater error than shorter distances, thus leading to relatively slower field speeds for faster anole species. The issue of escape distances will be dealt with in greater detail in another paper (Irschick, unpubl.), but our method of measuring distances from landmarks based on video footage ensures that longer distances will not be measured with more error than shorter distances, as they might tend to be if a stopwatch was used to measure speed, and distances were judged based on memory.

Previous studies have demonstrated that species and intraspecific classes (e.g., females, juveniles) behaviorally compensate for inferior sprinting capabilities by employing behaviors such as crypticity to avoid detection (Vitt and Cogdon 1978; Bauwens and Thoen 1981), or escape behaviors that do not rely solely on maximal sprinting ability (Martin and Lopez 1995). An alternative, and less studied means for slower species or intraspecific classes to compensate for their inferior sprinting capabilities during predator escape is for them to sprint closer to their maximal abilities than faster species or intraspecific classes.

This hypothesis of “compensation” assumes that there is a “cost” for lizards to sprint to their maximal capabilities in nature. That is, some reason must exist to explain why fast anole species do not sprint to the same percent of maximum performance as slow anole species. If such cost(s) exist, they likely are especially important to the faster anole species examined here (i.e., trunk-ground anoles), because these species also tend to be very conspicuous, usually perching on tree trunks in full view. Because trunk-ground anoles are conspicuous, it may be detrimental for them to sprint to their maximal capabilities every time a predator detects them. For example, fleeing repeatedly at top speeds may exhaust lizards, thus preventing them from effectively defending territories or capturing prey. On the other extreme, the slow twig anoles are both cryptic and extremely wary, and probably are discovered by predators less often than trunk-ground anoles. However, once discovered, a twig anole is at considerable risk of being eaten due to its poor sprinting abilities. In those rare instances in which a twig anole has been discovered, the benefits of fleeing effectively may outweigh any costs of sprinting to its maximal capabilities.

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**Literature Cited**


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