

The Evolution of Jumping Performance in Caribbean *Anolis* Lizards: Solutions to Biomechanical Trade-Offs

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ABSTRACT: Adaptationist theory predicts that species will evolve functional specializations for occupying different ecological niches. However, whereas performance traits are often complex, most comparative functional studies examine only simple measures of performance (e.g., sprint speed). Here we examine multiple facets of jumping biomechanics in 12 species of Caribbean *Anolis* lizards. These 12 species represent six ecomorphs, which are distinct ecological and morphological entities that have independently evolved on different Caribbean islands. We first show that the optimal angles for jumping maximum horizontal distances range from 39° to 42°, but the average jump angle of the 12 species is about 36°. Interestingly, these “sub-optimal” jumping angles result in only a small decrement in jump distance but substantial savings in flight duration and jump height. Further, our data show that the two key variables associated with increased jumping velocity (hindlimb length and takeoff acceleration) are independent of one another. Thus, there are two possible ways to achieve superior jumping capabilities: to evolve more muscular limbs—as stronger legs will produce more force and, hence, more acceleration—or evolve longer limbs. Our data show that anole species face trade-offs that prevent them from simultaneously optimizing different aspects of jumping ability but that they appear to have evolved behaviors that partially overcome these trade-offs.

Keywords: jumping, force platform, comparative, lizard, trade-offs.

A basic question in evolutionary biology concerns the manner in which species evolve functional specializations for occupying different habitats. Previous authors have stressed the importance of examining the evolution of function, morphology, and habitat use simultaneously (Huey and Bennett 1987; Lauder 1990, 1996; Losos 1990a; Wainwright 1994; Irschick and Losos 1998). While studies relating ecology to morphology (i.e., ecomorphology) are an important first step (see Wainwright and Reilly 1994 for an overview), data on how morphology relates to both performance and habitat use are important for fully understanding the adaptive process. This is because morphological differences do not always translate directly into differences in performance due to the potentially confounding role of behavior (Garland and Losos 1994; Lauder 1996; Lauder and Reilly 1996; Irschick and Garland 2001; Van Damme and Vanhooydonck 2001). This paradigm has most frequently been applied to locomotor capacities such as maximum sprinting or maximum endurance because they frequently are related to habitat structure (Irschick and Garland 2001). For example, Losos (1990a) showed that the ability of 14 Caribbean *Anolis* lizards to sprint quickly, cling well, and jump far was a significant predictor of habitat use (perch height and perch diameter). Despite the complexity of most performance traits, however, comparative studies often examine only simple measures of performance, such as maximum speed (e.g., Van Berkum 1986; Losos 1990a; Bauwens et al. 1995; Irschick and Losos 1999; Vanhooydonck and Van Damme 2001) or maximum endurance (Garland 1999; Vanhooydonck and Van Damme 2001).

This point is particularly relevant for jumping—which generally has been neglected by functional morphologists—because of the complex dynamics involved (Emerson 1985; Bels et al. 1992; Harris and Steudel 2002). A typical jump is characterized by several biomechanical variables, each of which could be ecologically important to a fleeing animal. For example, the maximum horizontal distance jumped may be important for effectively fleeing predators, but other variables (e.g., flight duration, the maximum height of a jump) may also be of consequence.

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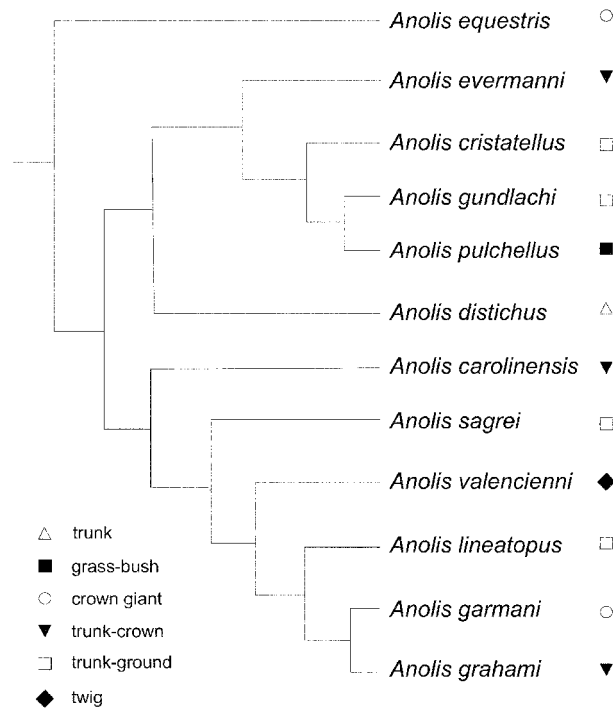


Figure 1: Phylogenetic tree depicting the relationships among the species used in our study. Symbols indicate the ecomorph categories by which species are classified. Based on data from Harmon et al. (2003).

Additionally, the quickness (i.e., acceleration and reaction time) of jumping may be of equal or greater significance when escaping predators. Of course, a more realistic scenario is one in which multiple variables are equally important to jumping animals. In this latter case it is probable that species will not be able to simultaneously optimize all jumping variables, and they will be faced with trade-offs among different components. However, to date, few studies have used a comparative approach to determine which of these vary among species, and thus we have a poor understanding of whether such trade-offs exist. Further, although many animals, such as primates, arboreal lizards, frogs, and carnivores, jump regularly, either when moving undisturbed or when escaping predators (Emerson 1985), only a few studies have examined how jumping performance relates to morphological variation among species (e.g., Moermond 1979a; Pounds 1988; Losos 1990a; Higham et al. 2001; Toro et al. 2003; but see Harris and Steudel 2002 for a detailed within-species study). We therefore know little about which aspect or aspects of the jumping response in animals are subject to adaptive differentiation among species.

Caribbean *Anolis* lizards have been the subject of numerous studies over the past 30 yr (e.g., Andrews and Rand 1974; Moermond 1979a; Losos 1994; Roughgarden 1995;

Irschick et al. 1997). Part of the reason for this interest is that anoles have undergone several independent adaptive radiations on each of the Greater Antillean islands (Williams 1983; Mayer 1989; Burnell and Hedges 1990; Powell et al. 1996; Losos et al. 1998; Jackman et al. 1999, 2002). Moreover, these radiations have largely occurred in parallel on each island, giving rise to groups of distantly related species that are similar both in morphology and habitat use. These groups, denoted “ecomorphs” by Williams (Rand and Williams 1969; Williams 1972, 1983; Losos 1990a), consist of six categories: twig, trunk, trunk ground, trunk crown, grass bush, and crown giants (fig. 1). Hence, although species within any given ecomorph category are similar in their ecology and morphology, each has evolved independently several times. The advantage of this system, therefore, lies in the enhanced statistical power provided by the independent evolution of phenotypes on different islands.

On a more general note, lizards have proven to be an excellent model system for the study of the evolution of performance capacities because of their willingness to run and jump and their high degree of variation in morphology, habitat use, and behavior (Moermond 1979a; Van Berkum and Tsuji 1987; Tsuji et al. 1989; Garland and Losos 1994; Sorci et al. 1995; Bonine and Garland 1999;

Irschick and Losos 1999; Melville and Swain 2000; Miles et al. 2000; Vanhooydonck et al. 2000; Higham et al. 2001; Van Damme and Vanhooydonck 2001). Furthermore, field and laboratory studies have shown that practically all *Anolis* species studied to date jump regularly when undisturbed, escaping a threat, or capturing prey (Moermond 1979b; Losos 1990a; Losos and Irschick 1996; Irschick and Losos 1998). Also, anole species differ dramatically in their relative hindlimb dimensions (Losos 1990a) and so are an excellent model system for studying jumping. Finally, recent work (Jackman et al. 1999, 2002; Harmon et al. 2003) has provided a phylogeny of many Caribbean anoles, thus enabling phylogenetic analyses.

Here we asked three specific questions. First, what are the actual jumping angles that anoles use, and how do these compare with theoretical expectations? To answer this question, we used Marsh's (1994) mathematical model (see "Methods"), adjusted to the particularities of lizard jumping, to calculate the optimal angle at which 12 different species of Caribbean *Anolis* lizards should jump in order to maximize the horizontal distance traveled. We then compared the optimal angles to the actual angles that each species used. We also tested whether these anoles exhibit trade-offs among jumping variables and determined which aspects of jumping are maximized during escape (e.g., flight duration, maximum horizontal distance, maximum acceleration). Second, how has body shape evolved to influence jumping capacity? Here we focus on the effects of morphology on the escape response as measured by jumping distance, velocity, acceleration, and power. Third, do anole ecomorphs differ in the biomechanics of jumping? While Losos (1990a) examined differences among ecomorphs in maximum jumping performance (horizontal distance), no studies have investigated whether anole ecomorphs differ in more detailed components of jumping ability. To address these issues, we measured the ability of 12 species of *Anolis* lizards to jump from a force platform in the laboratory and compared these biomechanical results with measurements of external morphology.

Methods

Subjects

We collected between three and 10 individuals from each of 12 species of *Anolis* lizards in the following localities: Discovery Bay marine laboratory, Jamaica (*Anolis lineatopus*, *Anolis grahami*, and *Anolis valencienni*); Miami, Florida (*Anolis garmani*, *Anolis sagrei*, *Anolis distichus*, *Anolis cristatellus*, and *Anolis equestris*); Luquillo National Forest, Puerto Rico (*Anolis gundlachi*, *Anolis evermanni*, *Anolis pulchellus*); and St. Charles Parish, Louisiana (*Anolis*

carolinensis; table 1). Lizards were transported from these localities and maintained at Tulane University facilities, where they were fed and watered ad lib. Using Mitutoyo calipers, for each animal we measured the morphological variables shown in table 1 to the nearest 0.01 mm and weighed them to the nearest 0.0001 g with a Denver instruments M-220 electronic balance.

Using a custom-made force plate, we recorded the forces generated by the lizards during jumping in three dimensions. Technical details of the force plate and jumping protocols can be found in Toro et al. (2003). Before each trial, lizards were placed in an incubator for at least 1 h at a temperature of 32°C except for *A. gundlachi*, which were maintained at 28°C (Hertz 1981, 1992; Huey and Webster 1976). Animals were placed on the force platform and induced to jump to a branch placed at the level of the force plate and just outside the presumed reach of the individual. Jumping was elicited by startling the animals with a sudden clapping of hands or a light tap on the tail.

Each animal was made to jump on five separate trials, preceded by at least 1 d rest. On every trial lizards were repeatedly induced to jump until showing signs of exhaustion. This typically meant that we obtained three good jumps per trial. Only the best jump out of all recordings was kept for analysis and assumed to be that individual's maximum performance.

We analyzed each jump with an algorithm written on Superscope 11 (3.0 pcc on a G4 Macintosh computer) that allowed us to calculate, from the force recordings in three dimensions, the kinematic variables shown in table 1. Details of this algorithm are explained in Toro et al. (2003).

Background on Jumping Dynamics

Marsh (1994) derived the following formula for calculating jump distance in frogs:

$$L_j = \frac{V_t^2 \sin \theta \cos \theta + V_t \cos \theta (V_t^2 \sin^2 \theta + 2gL_{cm} \sin \theta)^{0.5}}{g} + L_{cm} \cos \theta, \quad (1)$$

where L_j = distance jumped, V_t = takeoff velocity, θ = takeoff angle, g = acceleration due to gravity, and L_{cm} = distance from the tip of the outstretched hindlimbs to the center of mass (COM). In lizards, the COM is located roughly $H/2$ units of distance anterior from the hips (mean for 11 of the 12 species used in this study: $0.46H \pm 0.07H$ SD), where H is hindlimb length (fig. 3). Therefore, in our calculations L_{cm} becomes $1.46H$. Further, lizards bring their legs forward when preparing for a jump so that their toes are roughly under the COM (fig. 3b), and we must add this extra distance to the equation. Hence, Marsh's equation adjusted to lizard jumping becomes

Table 1: Origin, morphological, and performance data for the animals used in this study

| Species | Ecomorph | Origin | N | Performance variables | | | | | Morphological variables | | | | | | | | |
|----------------------------|----------|------------------|----|-----------------------|------------------|---------------------------|---|-------------------------|-------------------------|-------------|------------------|------------------|--------------|---------------|---------------|--------------------|------------------------|
| | | | | Angle (°) | Distance (cm) | Peak velocity (m/s) | Peak acceleration (m/s ²) | Peak power (W/kg) | Mass (g) | SVL (mm) | Hindlimb (mm) | Forelimb (mm) | Tail (mm) | Femur (mm) | Tibia (mm) | Metatarsus (mm) | Longest toe (mm) |
| <i>Anolis carolinensis</i> | TC | New Orleans, La. | 7 | 36.2 | 32.4 | 1.57 | 33.0 | 36.2 | 3.15 | 54.46 | 34.48 | 21.14 | 82.49 | 10.76 | 10.47 | 6.30 | 6.95 |
| | | | | 6.7 | 8.2 | .28 | 8.8 | 14.4 | 1.74 | 9.95 | 5.42 | 3.27 | 33.80 | 1.64 | 1.94 | 1.16 | .83 |
| <i>Anolis cristatellus</i> | TG | Puerto Rico | 6 | 39.1 | 42.7 | 1.81 | 38.1 | 47.5 | 7.02 | 63.13 | 50.29 | 30.42 | 75.69 | 15.83 | 15.18 | 8.90 | 10.37 |
| | | | | 5.5 | 9.2 | .24 | 7.1 | 13.9 | 2.31 | 6.36 | 6.61 | 3.44 | 22.50 | 2.22 | 1.59 | 1.43 | 2.48 |
| <i>Anolis distichus</i> | T | Miami, Fla. | 5 | 33.7 | 29.5 | 1.51 | 31.7 | 32.6 | 2.26 | 50.45 | 36.54 | 25.21 | 52.17 | 11.18 | 11.86 | 6.46 | 7.04 |
| | | | | 4.0 | 3.3 | .06 | 1.4 | 1.5 | .40 | 2.61 | 2.47 | 2.05 | 8.95 | 1.04 | .85 | .32 | .59 |
| <i>Anolis equestris</i> | CG | Miami, Fla. | 9 | 30.7 | 42.4 | 1.73 | 21.7 | 26.3 | 47.22 | 135.40 | 90.55 | 63.07 | 225.17 | 28.55 | 25.91 | 14.79 | 21.31 |
| | | | | 7.3 | 13.6 | .31 | 5.0 | 9.0 | 28.01 | 33.47 | 19.80 | 14.53 | 68.21 | 6.92 | 5.77 | 3.48 | 4.85 |
| <i>Anolis evermanni</i> | TC | Puerto Rico | 3 | 36.2 | 45.9 | 1.92 | 44.9 | 57.1 | 5.23 | 62.41 | 49.33 | 33.26 | 100.29 | 14.91 | 14.25 | 7.89 | 12.28 |
| | | | | 2.2 | 3.0 | .08 | .6 | 2.3 | 1.46 | 5.10 | 1.70 | 1.69 | 16.08 | .66 | .46 | .40 | .74 |
| <i>Anolis garmani</i> | CG | Miami, Fla. | 7 | 38.1 | 60.4 | 2.12 | 32.7 | 47.9 | 32.29 | 111.07 | 83.98 | 53.41 | 213.06 | 24.99 | 24.64 | 13.16 | 21.18 |
| | | | | 5.0 | 13.3 | .26 | 5.9 | 12.4 | 6.10 | 6.69 | 4.54 | 3.06 | 36.53 | 2.20 | 1.10 | .74 | 1.42 |
| <i>Anolis grahami</i> | TC | Jamaica | 4 | 39.1 | 46.3 | 1.90 | 40.6 | 52.4 | 7.13 | 62.81 | 47.96 | 30.33 | 99.96 | 15.09 | 14.14 | 7.58 | 11.15 |
| | | | | 4.7 | 7.6 | .19 | 5.2 | 11.2 | .87 | 1.84 | 2.64 | .73 | 8.87 | 1.27 | .78 | 1.02 | .80 |
| <i>Anolis gundlachi</i> | TG | Puerto Rico | 6 | 36.5 | 42.1 | 1.81 | 39.4 | 49.0 | 6.45 | 62.50 | 56.63 | 33.73 | 105.12 | 17.29 | 16.86 | 9.73 | 12.76 |
| | | | | 9.0 | 11.7 | .26 | 6.3 | 15.3 | 1.08 | 2.90 | 3.20 | 2.04 | 17.07 | 1.49 | .48 | .88 | 2.27 |
| <i>Anolis lineatopus</i> | TG | Jamaica | 10 | 36.3 | 45.5 | 1.90 | 40.5 | 51.7 | 5.52 | 59.31 | 49.65 | 30.24 | 86.51 | 15.54 | 14.52 | 7.76 | 11.83 |
| | | | | 7.1 | 14.1 | .28 | 4.7 | 9.6 | 1.14 | 2.58 | 2.11 | 1.18 | 34.73 | .86 | .67 | .61 | .71 |
| <i>Anolis pulchellus</i> | GB | Puerto Rico | 5 | 40.4 | 28.6 | 1.50 | 29.8 | 30.1 | 1.76 | 44.86 | 34.78 | 19.32 | 103.43 | 10.60 | 10.08 | 5.43 | 8.67 |
| | | | | 14.2 | 5.0 | .10 | 5.1 | 5.2 | .11 | .91 | 1.03 | 1.03 | 22.09 | .59 | .67 | .79 | .98 |
| <i>Anolis sagrei</i> | TG | Miami, Fla. | 9 | 40.1 | 35.0 | 1.69 | 36.7 | 40.8 | 3.93 | 51.59 | 37.56 | 21.92 | 84.83 | 10.57 | 11.50 | 7.43 | 8.07 |
| | | | | 15.5 | 10.7 | .22 | 8.9 | 13.0 | 2.60 | 8.06 | 6.57 | 4.20 | 25.66 | 1.83 | 2.22 | 1.15 | 1.64 |
| <i>Anolis valencienni</i> | TW | Jamaica | 8 | 30.8 | 35.5 | 1.70 | 33.3 | 38.4 | 6.19 | 71.38 | 37.84 | 25.22 | 87.35 | 12.46 | 11.64 | 6.81 | 6.95 |
| | | | | 6.5 | 6.4 | .13 | 3.6 | 7.4 | 1.17 | 3.34 | 2.32 | 1.75 | 8.25 | 1.05 | .78 | .47 | .40 |

Note: Top values in each row are the means; bottom values are standard deviations. SVL, snout-to-vent length; CG, crown giant; GB, grass bush; T, trunk; TC, trunk crown; TG, trunk ground; TW, twig.

$$L_j = \frac{V_i^2 \sin \theta \cos \theta + V_i \cos \theta (V_i^2 \sin^2 \theta + 2.92gH \sin \theta)^{0.5}}{g} + 1.46H \cos \theta + 0.46H. \quad (2)$$

Marsh (1994) added one more adjustment to this formula to account for the fact that takeoff velocity and angle are expected to be inversely correlated. This trend is expected because jumping at a steeper angle requires that more of the available work be put into simply lifting the animal's mass against gravity. We tested this assumption both among individuals of each *Anolis* species and across all individuals of all species. Within each of the 12 species, takeoff velocity and takeoff angle were not significantly related ($P > .05$ for all comparisons), and in two species in which the two variables approached significance, the relationship was weakly positive, not negative (*A. garmani*, $N = 7$, $R^2 = 0.55$, $P = .056$, slope = 0.70; *A. gundlachi*, $N = 10$, $R^2 = 0.31$, $P = .096$, slope = 0.43). Further, when pooling all 87 individuals across all species, the relationship between log-transformed takeoff angle and log-transformed takeoff velocity was marginally significant but positive ($R^2 = 0.05$, $P = .038$, $N = 87$; fig. 2). Importantly, takeoff angle only explained 5% of the variation in takeoff velocity, and even in the most extreme case (*A. valencienni*, where predicted and actual angles differ the most), taking this effect into account changed our predicted angle from 42° to 42.3° , a discrepancy of less than

1%. Therefore, we did not incorporate Marsh's last adjustment in our model, and formula (2) is the basis for all our calculations henceforward.

Statistical Analyses

We calculated the species means of all variables, log transformed them and entered them into PDTREE (Garland et al. 1999; Garland and Ives 2000) using the phylogeny shown in figure 1. The phylogeny in figure 1 was "pruned" from a phylogenetic analysis of a much larger number of anole species by Harmon et al. (2003). Consequently, because our phylogeny is only part of that larger phylogeny, we do not report bootstrap values, and this phylogeny is only a tentative hypothesis of the relationships of the 12 anole species. The larger tree in Harmon et al. (2003) is based on mitochondrial DNA sequences (the ND2 gene and associated transfer RNAs, equaling about 1,800 base pairs), all of which are present in GenBank. The larger tree in Harmon et al. (2003) was reconstructed using maximum likelihood without assuming a molecular clock and was then made ultrametric using nonparametric rate smoothing in the program TreeEdit (see Harmon et al. 2003 for details). Branch lengths are available on request from L. Harmon (harmon@biology.wustl.edu).

Using this tree, we calculated independent contrasts for all traits. This analysis is necessary because species are

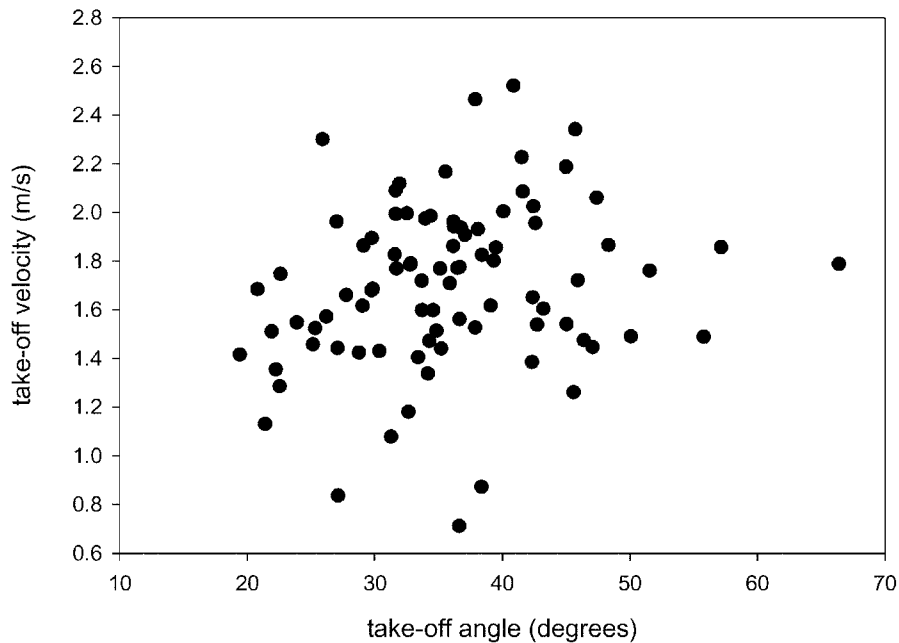


Figure 2: The relationship between takeoff angle and velocity for our study animals (all species pooled). Each point represents the maximum performance jump for a single animal ($R = 0.23$; $P = .038$; $N = 87$).

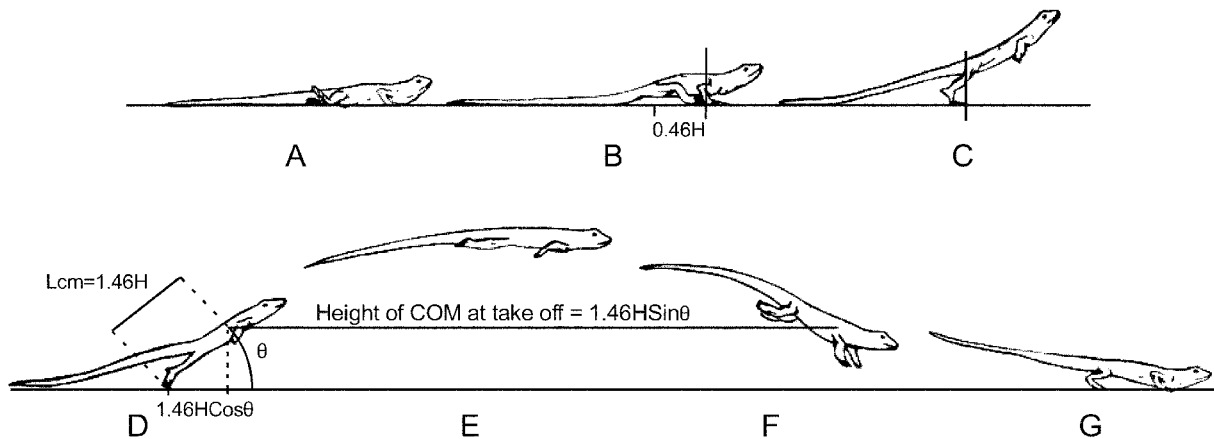


Figure 3: A typical anole jump. A, Normal standing position; B, preparatory forward movement of legs and lifting of the head; C, first phase of takeoff completed. The feet are now positioned directly underneath the pelvic girdle; D, takeoff; E, flight phase; F, crossing of takeoff height by the center of mass (COM) during landing; G, landing is highly variable but usually involves the forelimbs contacting the ground first.

related evolutionarily, and the value of any variable for a species is expected to be more similar to closely related species than to distantly related species (Felsenstein 1985).

We then size corrected all variables by calculating residuals of log-log linear regressions between each contrast and the contrast of snout-to-vent length (SVL, a standard linear measure of size for lizards) except for the variables “jump angle” and “peak power,” which displayed no significant relationship with size (linear regression of angle with SVL: $R^2 = 0.218$, $P = .147$, $N = 11$; linear regression of peak power with SVL: $R^2 = 0.001$, $P = .93$, $N = 12$). These new size-corrected variables were entered into a stepwise multiple regression to determine which variables were correlated with horizontal jump distance.

Measures of Habitat Use

To test whether ecomorphs differed in jumping variables, we conducted ANCOVAs with ecomorph classification as a predictor of each of the variables measured and SVL as a covariate (except in the case of angle and power, because of their lack of correlation with SVL). However, this procedure is problematic when using contrasts because of inflated Type I errors and reduced statistical power (Garland et al. 1993). Fortunately, Garland et al. (1993) provide a method for estimating F values, which can be compared with F statistics obtained in nonphylogenetic analyses. Based on a “known” phylogeny, the PDSIMUL computer program performs 1,000 simulations for the evolution of characters according to a given evolutionary model—brownian motion in our case—and tests for differences among groups. Each simulation produces an F value that is a consequence of the topology of the tree while not

accounting for evolutionary correlations among characters. This procedure creates a null distribution of 1,000 F values that can be used to test hypotheses while taking phylogeny into account. Consequently, we conducted the ANCOVAs on the raw data and used the PDAP package (Garland et al. 1993) to generate the empirical null distribution of F values for our analyses.

Results

Figure 3 shows a typical *Anolis* lizard jump. From a normal sitting position the animal prepares for the jump by bringing both legs forward and placing the feet in front of the center of mass while lifting the head (see Bels et al. 1992; fig. 3). The actual jump then begins with a forceful push maintained until takeoff, that is, loss of contact with the ground. Then comes the flight phase, and finally landing, which is usually completed forelimbs first, although this is highly variable.

Takeoff Angle

Figure 4 shows a landscape view of the theoretical optimal angle of takeoff as a function of hindlimb length and takeoff velocity calculated using equation (2). Also shown are points representing the actual values of V and H for each species used in the study. As figure 4 shows, the predicted optimal jump angle for all animals falls between 38.8° and 41.8° . However, the mean takeoff angle for all species is $36.4^\circ \pm 0.95^\circ$ (table 1; all reported values henceforth are mean \pm SE). There is a highly significant difference between the predicted and actual values of takeoff angles (paired sample t -test: $P < .001$, $t = 5.57$, $N = 12$).

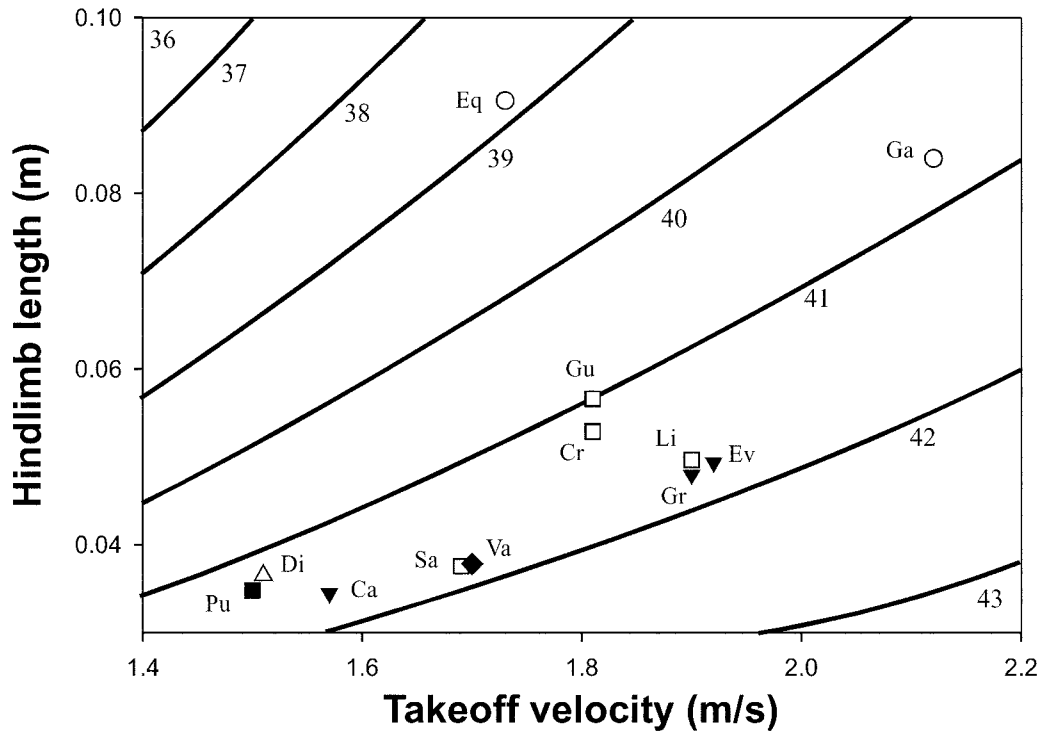


Figure 4: Landscape showing the theoretical optimal (i.e., distance maximizing) takeoff angle as a function of hindlimb length (H) and takeoff velocity (V). Each species is represented with its H and V coordinates. All predicted “optimal” takeoff angles fall within the 38.8°–41.8° range. Symbols as in figure 1.

We then calculated the losses each species incurred for horizontal distance, flight duration, and height attained by jumping at their actual jump angles and compared to an optimal-angle jump (table 2). While the average distance losses were small (mean among species = $1.4\% \pm 0.5\%$), both average duration ($7.4\% \pm 1.3\%$) and jump height ($15.1\% \pm 2.7\%$) changed considerably.

Morphology and Performance

As detailed in equations (1) and (2), the total distance jumped is the product of two performance variables: angle and velocity. Having dealt with takeoff angle, we now turn to velocity.

Table 3 shows the results of a stepwise multiple regression of hindlimb length, forelimb length, peak acceleration, body mass, and tail length as possible predictors of peak velocity (all variables size corrected). Only hindlimb length and peak acceleration were significant and positive predictors of takeoff velocity, explaining 78% of its variation. Moreover, as each variable in this multiple regression model is statistically independent of one another, variation in takeoff velocity explained by hindlimb length is

independent of the variation explained by acceleration capacity.

Animals with excellent jumping capacities often have long distal limb segments (e.g., Alexander 1968; Aerts 1998; see also Hildebrand 1985). To test whether species with the highest takeoff velocities tended to have disproportionately long distal limb segments, we calculated the residuals of regressions between hindlimb length as the independent variable and takeoff velocity and hindlimb segments as dependent variables (note that this analysis was run on the raw contrasts, not the size-corrected variables). The resulting variables thus represent hindlimb-length-free limb segments. For example, a positive value for the variable femur represents an animal whose femur is longer than another animal with the same total limb length regardless of whole-animal size. These residuals were then included in a stepwise multiple regression with hindlimb-free limb segments as independent variables and hindlimb-free takeoff velocity as dependent variables. None of the variables are significantly correlated with takeoff velocity (table 4). Therefore, once the effects of total limb length are controlled for, evolutionary changes in limb proportions do not seem to affect evolutionary changes in takeoff velocity.

Table 2: Distance, height, and time losses incurred by lizards jumping at the observed angles as compared to a distance-optimizing angle

| Species | Distance loss (%) | Height loss (%) | Duration loss (%) |
|----------------------------|-------------------|-----------------|-------------------|
| <i>Anolis carolinensis</i> | 1.4 | 17.2 | 8.3 |
| <i>Anolis cristatellus</i> | .2 | 7.3 | 3.6 |
| <i>Anolis distichus</i> | 2.5 | 23.6 | 11.4 |
| <i>Anolis equestris</i> | 2.5 | 24.9 | 11.4 |
| <i>Anolis evermanni</i> | 1.4 | 17.8 | 8.5 |
| <i>Anolis garmani</i> | .3 | 8.2 | 4.1 |
| <i>Anolis grahami</i> | .3 | 8.6 | 4.2 |
| <i>Anolis gundlachi</i> | .9 | 14.2 | 6.9 |
| <i>Anolis lineatopus</i> | 1.3 | 17.2 | 8.3 |
| <i>Anolis pulchellus</i> | .0 | 2.9 | 1.7 |
| <i>Anolis sagrei</i> | .1 | 5.4 | 2.8 |
| <i>Anolis valencienni</i> | 5.6 | 34.6 | 17.1 |
| Mean | 1.4 | 15.1 | 7.4 |
| SE | .5 | 2.7 | 1.3 |

Note: Losses in height and duration are much greater than for distance.

Ecological Correlates

Table 5 shows the results of ANCOVAs comparing different ecomorphs for various performance variables with SVL as covariate where appropriate. Once differences in size were accounted for, ecomorphs did not differ significantly in any aspect of jumping performance (see also fig. 5 for a typical example of the distribution of ecomorphs around the expected value for a given jump variable).

Discussion

The Evolution of Trade-offs in Jumping: Takeoff Angle

The study of performance capacities has played a central role in our understanding of evolutionary adaptation because of their importance for organismal survival (Arnold 1983; Pough 1989; Garland and Losos 1994; Wainwright 1994; Irschick and Losos 1998; Irschick and Garland 2001). According to this view, species presumably strive to perform well in many disparate tasks, but various studies have found that trade-offs are inherent in functional systems (Webb 1984; Wainwright 1994; Aerts et al. 2000; Vanhooydonck and Van Damme 2001; but see Huey and Hertz 1984), often resulting in good performance at one task but poor performance at another. Such trade-offs can profoundly shape the direction of evolution if they prevent a species from optimizing two or more potentially important aspects of performance. In the case of jumping in anoles, a lizard should ideally want to move away from a threat by maximizing horizontal jump distance to get as far away from the predator as possible, and minimizing flight time, thereby allowing it to change its direction of movement.

Concurrently optimizing the two is not possible, however, due to the influence of jump angle on both variables. Steep jumps tend to be long jumps, but they contain a time-consuming flight phase; shallow jumps, on the other hand, have short flight times but result in short horizontal jump distances. If both facets of jumping performance are important to anoles, one might expect a compromise phenotype (Lewontin 1978; Vanhooydonck et al. 2001).

Indeed, our data show that anoles may have evolved an elegant solution to this trade-off by taking advantage of the physics of parabolic movement. Based on theoretical considerations, we showed that the takeoff angle that maximizes horizontal distance for the 12 lizard species varies between 38.8° and 41.8°, but these species actually jump at significantly lower angles (36.4°, with some departures; see below). By assuming the small distance loss (mean among species = 1.4%) that this takeoff angle induces, anoles reduce their flight time (loss = 7.4% among species) and maximum height (loss = 15.1% among species; table 2) disproportionately. For every percentage unit of distance lost, lizards reduce flight time by 5% and height by 10%. In this manner, the trade-off between jump distance and flight time is largely overcome. Of course, future studies (e.g., enclosure studies with a predator) should be conducted to reveal which, if any, of these variables is important for various ecologically relevant activities (predator escape, prey capture). Such studies can also test whether anoles actually jump at the observed suboptimal angles in nature, and if so, whether they provide an advantage in ecologically relevant situations.

An important consideration is that these calculations are not specific to *Anolis* lizards and should apply to all jumping animals with an important propulsive phase. Indeed, R. L. Marsh has noted that “the frog can take off over a broad range of jumping angles and still achieve nearly maximal distance” (Marsh 1994, p. 57). Thus, it would be interesting to examine whether other animal species tend to jump at suboptimal angles.

While this general trend holds among all of the species

Table 3: Results of a multiple regression of performance and morphological variables as predictors of takeoff velocity

| | Standardized | | | |
|---------------------|--------------|---------|-------|------|
| | N | β | t | P |
| Variables included: | | | | |
| Max acceleration | 11 | .522 | 2.898 | .020 |
| Hindlimb length | 11 | .504 | 2.799 | .023 |
| Variables excluded: | | | | |
| Forelimb length | 11 | -.081 | -.194 | .852 |
| Mass | 11 | .079 | .264 | .799 |
| Tail length | 11 | .101 | .573 | .584 |

Note: All variables are standardized size-corrected contrasts. The model's adjusted R² = 0.78.

Table 4: Results of a stepwise multiple regression of leg segments as possible predictors of takeoff velocity

| Independent variable | <i>N</i> | <i>R</i> ² | <i>F</i> | <i>P</i> |
|----------------------|----------|-----------------------|----------|----------|
| Femur | 11 | .310 | .286 | .606 |
| Tibia | 11 | .003 | .026 | .875 |
| Metatarsus | 11 | .034 | .315 | .588 |
| Longest toe | 11 | .025 | .231 | .642 |

Note: All variables are hindlimb-size-free standardized contrasts.

examined, certain anoles that occur in unusual habitats show some departures. The most notable was the twig anole *Anolis valencienni*, a species that inhabits dense bushes and trees. Previous studies have shown that anoles inhabiting dense habitats tend to jump more frequently (Moermond 1979a; Pounds 1988) and make shorter jumps, typically between adjacent surfaces. In such dense surroundings, shallow jumps may be important because of the need to avoid obstacles. Indeed, *A. valencienni* used a very low takeoff angle (30.8°) that resulted in rather high distance losses (5.6%) and a maximum height of only two-thirds that of optimal jumps. Thus, for some anole species, jumping long distances may be less important than jumping accurately.

The Evolution of Trade-offs in Jumping: Morphology

A central tenet of adaptationist theory is that evolutionary changes in morphology or structure should be closely linked to evolutionary changes in performance (Losos and Miles 1994; Larson and Losos 1996). Theoretical models predict that animal species with relatively long hindlimbs should exhibit high takeoff velocities and accordingly jump farther (Alexander 1968; Bennet-Clark 1977; Emerson 1985; Harris and Steudel 2002) because longer limbs increase the distance and time through which the animal can accelerate. This prediction is supported by our data and conforms to several other experimental studies (Rand 1952; Zug 1972; Dobrowolska 1973; Emerson 1991; Choi and Park 1996; Harris and Steudel 2002).

Takeoff velocity can also be affected by acceleration capacity (table 3; and indeed, acceleration being the derivative of velocity, the relation is obvious). These high accelerations are, in turn, the result of a higher force production relative to body mass, as acceleration is force per unit mass by definition. Increased force may be obtained in one of two ways: the first is to alter the physiology of jumping muscles, allowing an animal to produce more work per unit of mass; the second is to increase the relative mass of these muscles. Recent experiments on cats hint that the former may not be common (Harris and Steudel

2002), perhaps because of prohibitive energetic requirements of “enhanced” muscles (but see Choi and Park 1996). More detailed histological and in vitro performance studies are needed to test this hypothesis for anoles. Nevertheless, the striking differences in robustness among anole species (e.g., Higham et al. 2001) suggest that increases in limb extensor muscle mass are a more probable evolutionary scenario.

An interesting finding of our study was that evolutionary increases in hindlimb length were not correlated with evolutionary increases in acceleration capacity despite the fact that both are correlated with jumping velocity (table 3). This suggests that there exist two independent strategies for increasing jump velocity, namely, having longer or more muscular (thicker) legs or both. This trend may have important ecological implications, especially in light of studies that show that relative limb length is related to the ability to move effectively on surfaces of different diameters (Losos and Sinervo 1989), an important ability for anoles (Irschick and Losos 1999). Specifically, Losos and Sinervo (1989) showed that short-limbed species run well on narrow surfaces whereas long-limbed species run poorly and often stumble on narrow surfaces. Interestingly, our results suggest that anoles that live on narrow perches are not doomed to be poor jumpers but can evolve short but thick legs that are well suited for both running on narrow perches and also jumping.

Previous authors have also posited a positive relationship between the relative size of the most distal limb segments and the ability to run quickly and jump far, particularly in mammals (Alexander 1977; Aerts 1998). Theoretically, longer and lighter distal segments should

Table 5: Results of ANCOVAs between ecomorph classification and size-corrected performance variables with snout-to-vent length (SVL) as covariate

| Model (dependent variable, covariate) ^a | <i>F</i> statistic | Critical <i>F</i> value ^b | <i>P</i> |
|--|--------------------|--------------------------------------|----------|
| Takeoff angle, not correlated ^c | 2.099 | 3.66 | .166 |
| Jump distance, SVL | .726 | 3.98 | .602 |
| Maximum velocity, SVL | .652 | 3.79 | .627 |
| Maximum acceleration, SVL | 1.179 | 4.09 | .413 |
| Peak power, not correlated ^c | 1.234 | 4.18 | .373 |

Note: These analyses were run on the raw data and not the independent contrasts, as explained in the “Methods” section.

^a Independent variable = ecomorph; *N* = 11.

^b *F* values were empirically calculated using simulations as explained in the text.

^c These variables were not correlated with SVL (see text).

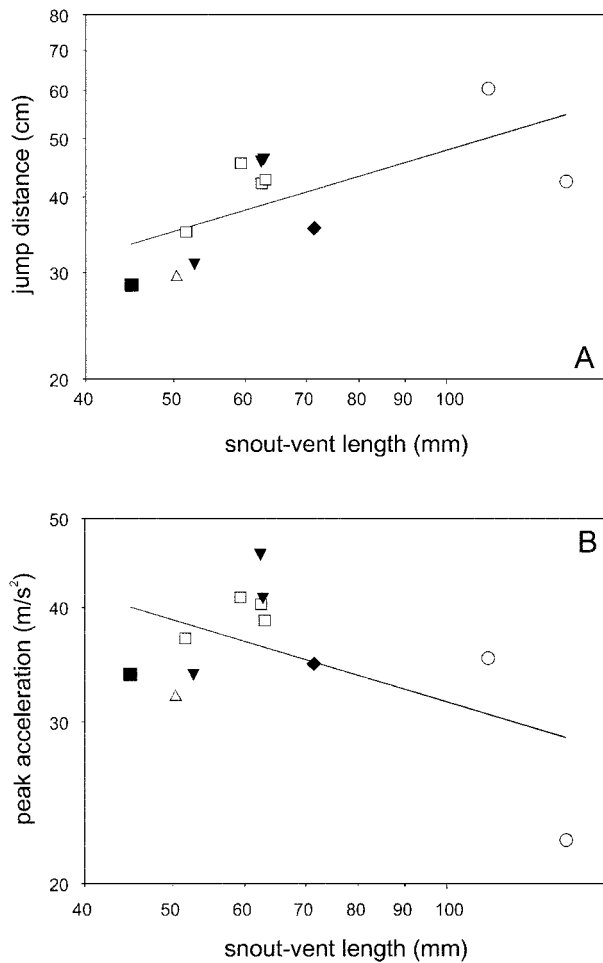


Figure 5: A, Linear regression of maximum jump distance as a function of size (snout-to-vent length). B, Linear regression of maximum acceleration capacity as a function of lizard size. Note the homogeneous distribution of ecomorphs around the regression line. Symbols as in figure 1.

induce less rotational inertia on the limbs, thus enabling higher takeoff velocities (see Hildebrand 1985 as well). However, our results show that, at least in *Anolis* lizards, it is the total length of the limb that matters and not its proportions (table 4). This finding could be a consequence of the small size of *Anolis* lizards in general (all species in this study were less than 100 g in mass). Indeed, scaling models suggest that as animals grow larger, the relative force output will decrease (see, e.g., Vogel 1988; but see Meyers et al. 2002), forcing larger species to evolve efficient ways to accomplish functional tasks with relatively little available force. Thus, one possibility is that anoles are so small that the rotational inertia of the legs does not pose a major functional problem. Alternatively, rotational inertia might not be an issue for onetime explosive move-

ments such as jumping but may rather only become important during cyclical movements as in cursorial mammals. In vivo muscular work or kinetic studies of locomotor performance could shed light on this issue.

Coevolution of Jumping Biomechanics and Ecology

Previous studies have shown that anole ecomorphs differ in many ecological, morphological, and performance variables (Moermond 1979a; Losos 1990a, 1990b; Irschick and Losos 1998, 1999), and anoles now serve as classic examples of convergent evolution (e.g., Begon et al. 1998). Consequently, one surprising result from our work was that the ecomorphs sampled did not differ significantly in various measures of jumping ability (table 5). This is intriguing because Losos (1990a) reported significant differences in the maximum horizontal distance jumped for several of the same species examined here. However, his study was based on a principal components analysis of three performance measurements—jumping, running, and clinging—and on closer inspection, his work shows that clinging ability was the primary separator of ecomorphs. Thus, we conducted a phylogenetically corrected ANCOVA (with SVL as covariate) using the jumping data reported in Losos (1990a) and found that although the ecomorphs tended to differ in jumping ability, the difference was marginally nonsignificant ($F = 4.12$, $P = 0.07$, $N = 14$). Moreover, the near significance of this result was heavily dependent on the inclusion of the twig anole *Anolis occultus*, an extremely poor jumper that we were unfortunately not able to include in our study. When we excluded *A. occultus* from the analysis of Losos's data, the anole ecomorphs clearly did not differ ($F = 1.48$, $P = 0.43$, $N = 13$). Thus, inclusion of a larger number of anole species representing each ecomorph type (e.g., *A. occultus* representing the twig anoles) would be useful in determining the degree to which anole ecomorphs actually differ in jumping capacity.

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