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# THE QUICK AND THE FAST: THE EVOLUTION OF ACCELERATION CAPACITY IN *ANOLIS* LIZARDS

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*Abstract.*—Although of prime ecological relevance, acceleration capacity is a poorly understood locomotor performance trait in terrestrial vertebrates. No empirical data exist on which design characteristics determine acceleration capacity among species and whether these design traits influence other aspects of locomotor performance. In this study we explore how acceleration capacity and sprint speed have evolved in *Anolis* lizards. We investigate whether the same or different morphological traits (i.e., limb dimensions and muscle mass) correlate with both locomotor traits. Within our sample of *Anolis* lizards, relative sprint speed and acceleration capacity coevolved. However, whereas the variation in relative acceleration capacity is primarily explained by the variation in relative knee extensor muscle mass, the variation in relative sprint speed is correlated to the variation in relative femur, tibia, and metatarsus length as well as knee extensor muscle mass. The fact that the design features required to excel in either performance trait partly overlap might explain the positive correlation between the variation in relative sprint speed and acceleration capacity. Furthermore, our data show how similar levels of sprint performance can be achieved through different morphological traits (limb segment lengths and muscle mass) suggesting that redundant mapping has potentially played a role in mitigating trade-offs.

*Key words.*—Ecomorphology, interspecific, comparison, locomotion, muscle, performance.

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Although rarely empirically demonstrated, locomotor performance is believed to be a crucial determinant of organismal fitness (see LeGalliard et al. 2004; Miles 2004; Husak 2006). Not surprisingly, the study of locomotor performance, in all its facets, has undergone explosive growth over the last decades. During this time, a wealth of data has become available on how genetics, morphology, physiology, kinematics, behavior, and ecology affect locomotor performance (reviews in Bennett and Huey 1990; Garland and Losos 1994; Irschick and Garland 2001; Autumn et al. 2002; Biewener 2002). One aspect most of these locomotion studies share is that they focus on steady-state locomotion in which movement is typically linear and uniform (i.e., at a constant speed). In nature, however, animals often show intermittent locomotion, including pauses alternating with fast and unpredictable bursts of movement (see Kramer and McLaughlin 2001; Weinstein 2001). Although non-steady-state locomotion, during which movement is nonuniform and typically unpredictable (i.e., accelerating and decelerating bouts), is thus likely of prime ecological relevance, it has hardly been investigated in detail (Garland and Losos 1994).

Surprisingly, an extensive literature search revealed no empirical data on which functional characteristics actually determine acceleration capacity among species, and how. In addition, it is unclear whether the design traits determining acceleration capacity influence other aspects of locomotor performance (e.g., sprint speed) as well. Depending on the functional relationship between design features and different locomotor performance traits, the respective performance traits will be intercorrelated in one of the following three ways. First, if both performance traits are determined by the same functional design, they are predicted to coevolve in a positive manner. Second, if the two performance traits pose conflicting demands on the same design features, excellence in one performance trait will be achieved at the cost of high performance in the other, resulting in a negative correlation between the two performance traits. Third, if different nonconflicting design traits underlie either performance trait, or if different combinations of design traits result in similar performance capacities, performance traits will evolve independently from one another. Moreover, by investigating how different performance traits are intercorrelated, insights may be gained into the structure-function relationships underlying both locomotor performance traits.

In a first attempt to understand the evolution of acceleration capacity, we study how sprint speed and acceleration capacity are functionally related among different species of *Anolis* lizards. To date, one empirical study has suggested that speed and acceleration capacity are positively correlated among individuals within one lizard species (Huey and Hertz 1984). Based on this study, other researchers have assumed a positive relationship between speed and acceleration for all terrestrial vertebrates. However, in the one species for which extensive acceleration data is available, namely humans, acceleration capacity and maximum running speed appear to be specific qualities that are relatively unrelated to one another (Little and Williams 2005). Moreover in human sprinters, prior studies have shown that the acceleration phase and the maximum running speed phase in a 100 m race rely on conflicting requirements: improvement of maximal speed requires lower moments of inertia of the leg and thus less muscle mass situated distally, whereas faster acceleration re-

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quires more muscle mass (Delecluse 1997; see also Hildebrand 1985).

In addition, body size may have opposing effects on speed and acceleration. Although sprint speed generally increases with size (review in Garland and Losos 1994; Van Damme and Vanhooydonck 2001), large animals are predicted to be relatively bad at accelerating in comparison to small animals (Hill 1950). Hill (1950) argued that the negative effect of body size on acceleration performance is due to the differential scaling of mass and muscular force. Whereas mass scales to length to the third power, muscular force scales to length to the second power. Since acceleration capacity equals force divided by mass, it is predicted to scale to length to the inverse power (Hill 1950). However, empirical data on the effect of body size on acceleration capacity remains ambiguous (e.g., Huey 1982; Huey and Hertz 1984; Emerson 1991; Carrier 1995; Toro et al. 2003).

Last, at the level of the design of the muscular and musculoskeletal system, force generation and velocity may trade off because muscles and musculoskeletal systems that are designed for fast contractions inevitably produce less force. This may result in a negative relationship between force and velocity at the whole-animal level. Since force and acceleration are tightly related (force = mass × acceleration), the force-velocity trade-off may in turn lead to a trade-off between acceleration and speed. The mechanics of simple lever systems, such as the jaws of fishes and the claws of crabs, corroborate this idea (Westneat 1994; Schenk and Wainwright 2001; Levinton and Allen 2005).

Although some biomechanical principles suggest that speed and acceleration should trade off because they pose conflicting demands on the same design traits, recent theoretical evolutionary models have demonstrated that the same performance may potentially be achieved through many different pathways. Moreover, design traits are often redundant (Alfaro et al. 2004, 2005; Wainwright et al. 2005; see also Koehl 1996). As a consequence, optimizing multiple design traits simultaneously, without detrimentally affecting all associated performance traits, is theoretically possible. So-called many-to-one mapping of form and function may thus result in greater evolutionary flexibility and mitigate evolutionary constraints imposed by design trade-offs (Alfaro et al. 2005; Wainwright et al. 2005). At the moment, empirical evidence for many-to-one mapping is scarce. Wilson et al. (2002) showed that whereas power output and fatigue resistance in frog limb muscles trade off, swimming speed and endurance were not correlated. This finding suggests at least some degree of redundancy in the traits determining whole-organism performance. Similarly, comparative work on *Anolis* lizards showed that similar jumping capacities can be achieved by combining different limb lengths and limb robustness (used as a proxy for muscle mass). The redundant mapping of jumping capacity thus may lead to a relaxation of the trade-off between sprinting and jumping ability, since lizards with short and stocky legs will be agile runners on narrow perches and good jumpers at the same time (Toro et al. 2004).

In this study, we test how sprint speed and acceleration capacity are related by examining the evolutionary intercorrelation between sprint speed and acceleration capacity among 16 *Anolis* lizard species. We use *Anolis* lizards as our study system because they typically use short and unpredictable locomotor bouts during predator escape, foraging, and social interactions (Irschick and Losos 1998, 1999). In addition, *Anolis* lizards have evolved independently at least four times into a series of ecologically, behaviorally, and morphologically distinct forms called ecomorphs (e.g., Losos et al. 1998). To understand the nature of the speed-acceleration relationship, we determine which morphological characters correlate to acceleration capacity and sprint speed, respectively. We first test how body size (snout-vent length) relates to sprint speed and acceleration capacity in our sample of lizard species, because theoretical biomechanical models suggest that both performance traits may be affected by size in opposing ways (see above). Second we examine how differences in shape affect speed and acceleration capacity. In addition to taking ''traditional'' limb length measurements (e.g., hind limb length; see Losos 1990; Garland and Losos 1994; Beuttell and Losos 1999), we include, for the first time, comparative data on muscle mass. In the past, the variation in sprint speed has been shown to be correlated to the variation in limb (segment) length (e.g., Garland and Losos 1994; Irschick and Jayne 1998; Vanhooydonck et al. 2002), but myological, kinematic, and electromyographic data suggest an important role for the limb muscles as well (Snyder 1954; Reilly 1995; Reilly and Delancey 1997; Nelson and Jayne 2001). Also, muscular traits are believed to be of prime importance in determining acceleration capacity in lizards (Curtin et al. 2005; see also Delecluse 1997).

## MATERIALS AND METHODS

### *Animals*

Between November 2001 and June 2002, we captured male individuals of 16 different *Anolis* species by hand or noose at different localities. One of the species, *A. cristatellus*, was sampled in two populations (see below). These 16 species were selected because they represent six different ecomorphs (cf. Williams 1983; Losos 1990; Beuttell and Losos 1999; Appendix 1 and 2). On mainland United States; we caught *A. carolinensis* (New Orleans, LA), *A. sagrei*, *A. distichus*, *A. equestris*, *A. garmani*, and *A. cristatellus* (all Miami, FL); *A. grahami*, *A. lineatopus*, and *A. valencienni* were caught in Jamaica (Discovery Bay); and *A. cristatellus*,, *A. cuvieri*, *A. evermanni*, *A. gundlachi*, *A. krugi*, *A. occultus*, *A. pulchellus*, and *A. stratulus* were all from Puerto Rico (El Verde and Cambalache forests).

The nine species from mainland United States and Jamaica were transported back to the laboratory at Tulane University, New Orleans, Louisiana. Upon arrival in the laboratory, the lizards were housed in pairs in 40-L terraria lined with leaf litter and with a dowel. Terraria were placed in a temperature-controlled room (29 ± 2°C) illuminated 12 h per day. We fed the animals live crickets dusted with calcium and vitamin supplements three times a week; they were sprayed with water daily.

The species from Puerto Rico were taken to the field lab at El Verde upon capture and their performance (see below) was tested on the same or following day (except for *A. cuvieri*, see below). Morphological measurements were taken immediately after the running trials. Lizards were kept in individual plastic bags while they were held at the field station. They were released at the site where they had been caught within 48 h.

### *Morphology*

We took the following measurements using digital calipers (Mitutoyo [Telford,u.k.] CD-15DC; accuracy of 0.01 mm): snout-vent length (SVL; measured from tip of snout to cloaca), femur length (measured from hip to knee), tibia length (measured from knee to ankle), and metatarsus length (measured from ankle to base of second hind toe).

One to three individuals per species (see Appendix 1) were sacrificed using an overdose of ketamine (excluding *A. occultus* and *A. cristatellus* from Puerto Rico). They were subsequently preserved in 10% aqueous formaldehyde (24 h) and stored in ethanol (70%) for at least three months prior to dissection. Of these specimens, all hind limb muscles of the right hind limb were dissected. We classified the muscles into nine functional groups: femur protractors, femur retractors, femur abductors, femur adductors, knee flexors, knee extensors, ankle flexors, ankle extensors, and other muscles (e.g., rotators). Muscles were weighed per functional group on a Mettler (Greifenseu, Switzerland) MT5 electronic balance (0.001 mg). Because all individuals were stored in alcohol for such a long period of time, we assume that all muscles regardless of their volume were dehydrated to the same extent. This procedure, therefore, reduced the possibility of artifacts in the interspecific comparison of muscle masses. For the purpose of this paper, we only include data on femur retractor muscle mass and knee and ankle extensor muscle mass because these are the muscle groups predominantly responsible for generating propulsion during locomotion (see Reilly 1995; Nelson and Jayne 2001).

### *Performance Trials*

#### *Laboratory*

We induced lizards to run up a plastic dowel (0.08 m diameter) covered with mesh, by clapping hands and/or tapping the lizards slightly on the base of the tail. The dowel was 2 m long and placed against the wall at an angle of 45°. We placed a reference grid of 0.2 m × 2 m, consisting of squares of 5 cm × 5 cm, alongside the dowel. Lizards were filmed in lateral view over a distance of 1 m using a high-speed video camera (Redlake [Tucson, AZ] Motionscope PCI camera) set at 250 frames $\text{sec}^{-1}$. Filming at this frame rate has been shown to be sufficiently accurate (cf. Walker 1998), particularly for the accelerations and velocities observed in this study (cf. Bergmann and Irschick 2006). We placed the lizards on the dowel so that the lizard was just in view. We performed between five and 10 trials per individual, on several nonconsecutive days. Prior to experimentation and in between trials, the lizards were placed in an incubator set at 32°C for at least one hour to attain body temperatures similar to their preferred field body temperatures (see also Toro et al. 2003).

#### *Field*

Puerto Rican species were filmed either in the forest where they were captured (*A. cuvieri*) or at the field station (all other species). The experimental design used to film the lizards differed only slightly from the experimental setup in the lab. The dimensions of the dowel were identical. At the field station, the dowel was placed against a wall; in the forest, it was placed against a tree trunk (both at an angle of 45°). We filmed the lizards at 240 frames $\text{sec}^{-1}$ using a JVC (Yokohama, Japan) high-speed camera (model GR-DVL9500U). Prior to experimentation and in between trials, the lizards were placed in individual plastic bags outside in the shade to attain body temperatures close to the environmental temperatures. At least five runs were recorded per individual on the same or on consecutive days.

After filming, we selected all ''good'' sequences per individual. A good sequence was defined as one in which the lizard started from a complete standstill, ran nonstop over a distance of at least 0.20 m (except for *A. occultus*, see below), and ran on top of the dowel, in a straight line. For these sequences, the tip of the snout was digitized at 250 frames $\text{sec}^{-1}$ (240 frames $\text{sec}^{-1}$ for Puerto Rican species) using Peak Performance MOTUS software. (ViconPeak, Oxford, U.K.) At the beginning of each sequence, we digitized four points a known distance apart on the reference grid. We started the frame-by-frame digitization 20 frames before the first movement (i.e., lizard sitting still) and we stopped when the lizard stopped running or ran out of view. The XY coordinates obtained from the digitizations were then smoothed using the quintic spline processor (QSP) implemented in the MOTUS software. The routine fits the fifth degree polynomial to the displacement data and smoothes them based on an estimate of the error variance. The error variance depends on the nature of the data and is estimated for each sequence that is analyzed. We chose to use the QSP because in this routine the derivatives are computed directly from the spline coefficients, and instantaneous velocity and acceleration are subsequently calculated (see also Bergmann and Irschick 2006). However, the QSP method consistently underestimates maximal acceleration (Walker 1998).

We subsequently inspected all acceleration profiles visually and discarded those sequences for which the profile showed a scattered or random pattern. As an estimate of an individual's maximal acceleration capacity, we used the highest instantaneous acceleration attained by that individual in any of the trials. However, if the highest acceleration out of all trials for a given individual equaled or was greater than 200% of the second highest acceleration for that individual, we discarded the former estimate and used the latter in further analyses. We noted, per individual, in which trial it attained the highest acceleration.

Based on the instantaneous displacement data, we calculated, for each sequence, the average sprint speed over 0.20-m intervals using a QBasic program custom-written by R. Van Damme. In this program, the time it takes a lizard to cover any 0.20-m interval out of the total distance of 1 m (i.e., total distance over which we filmed) is calculated. Sprint speed is subsequently calculated by dividing 0.20 m by the time it takes to cover this distance. This estimate of sprint

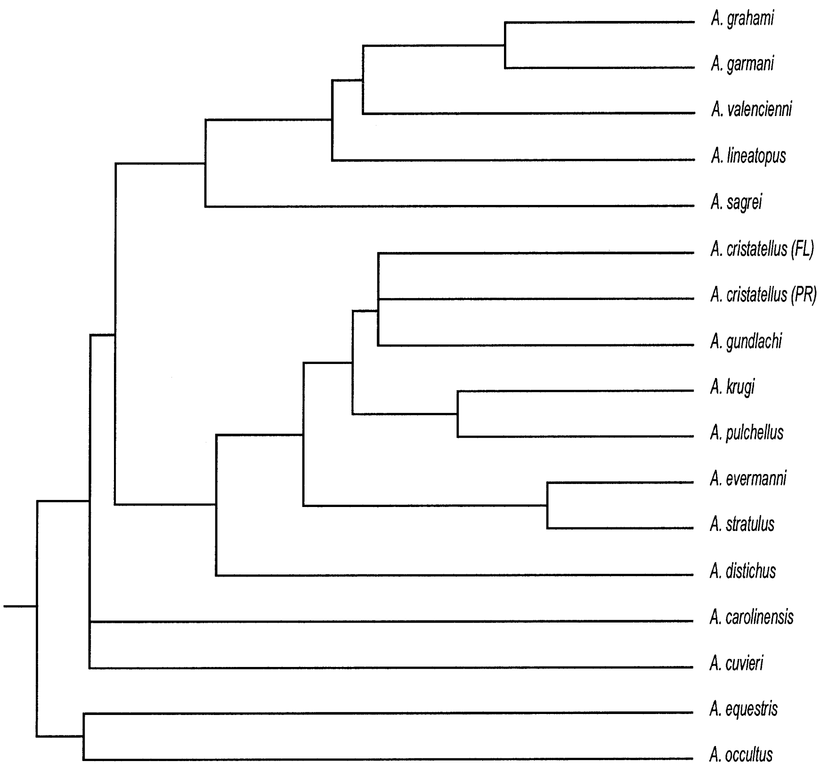

FIG. 1. Phylogenetic relationships among the 16 *Anolis* species used in this study. The phylogenetic tree is based on mitochondrial DNA (Nicholson et al. 2005). In the analyses, the node connecting the two *cristatellus* populations was placed as deep as possible for the two populations to still be monophyletic (L. Harmon, pers. comm.). Branch lengths are to scale.

speed is similar to measurements of sprint speed using electronic racetracks (cf. Huey et al. 1981; Garland and Losos 1994) and represents a measure of average sprint speed over a given distance. As an estimate of an individual's maximal sprint speed, we used the highest speed attained over any 0.20-m interval in any trial for that individual. We noted, per individual, in which trial it reached the highest sprint speed. Since we were unable to obtain recordings of *A. occultus* individuals running nonstop over more than 0.10 m, we calculated average speed over 0.10-m intervals for this species.

Although lizards typically reach maximal sprint speed within 0.30 m after starting from a standstill (Huey and Hertz 1984; B. Vanhooydonck, pers. obs.), it remains unclear whether all individual lizards reached their maximal attainable speed in our trials. To make sure the sprint speed-acceleration relationship based on our speed data was valid, we tested whether similar results were obtained when using maximal sprint speeds from Losos (1990). In this paper, maximal sprint speeds for 12 of the 16 species under study were measured on a 2.25-m long flat electronic racetrack, angled up at 37° (Losos 1990).

Subsequently, we checked, per individual, in which trial it attained the highest acceleration and in which the highest speed. In 73% of all cases, individual lizards achieved the highest (individual) acceleration and speed in a different trial. For those cases in which the individual maximum at both performance traits was reached in the same sequence, we randomly used either the second highest acceleration or the second highest speed for that individual in subsequent analyses. In doing so, we circumvent the potential problem of interdependency of the two performance measures.

### *Statistical Analyses*

Average values per species were calculated for all variables and species, and the averages were logarithmically ($\log_{10}$) transformed.

Because species share parts of their evolutionary history, they cannot be regarded as independent datapoints in statistical analyses (Felsenstein 1985, 1988; Harvey and Pagel 1991). However, various methods and computer programs have been developed over the years, in which phylogenetic relationships among different species are taken into account in statistical analyses (Felsenstein 1985, 1988; Harvey and Pagel 1991; Losos and Miles 1994). In this study, we use both Monte Carlo simulations (Garland et al. 1993) and the independent contrast approach (Felsenstein 1985, 1988).

Both the simulation and the independent contrasts approach require information on the topology and branch lengths of the phylogenetic tree. The phylogeny of the 16 *Anolis* species under study here is based on a phylogenetic analysis of a much larger number of anole species by Nicholson et al. (2005), using mitochondrial DNA sequences (Fig. 1). Branch lengths are available from the internet (http://biosgi.wustl.edu/~lososlab/anolis_mbg_2005) and upon request from K. Nicholson. The node connecting the two *cristatellus* populations was placed as deep as possible for the two populations to still be monophyletic (L. Harmon, pers.

comm.). To check whether branch lengths were adequate, we tested whether the absolute values of the standardized contrasts were correlated to their standard deviations (PDTREE program; Garland et al. 1999). Only in one case was the correlation significant, indicating that branch lengths are not adequate. We therefore transformed the branch lengths using a rho transformation with rho equal to 0.01 (PDTREE program; Garland et al. 1999).

### *Ecomorph differences*

We tested whether ecomorphs differ in acceleration capacity and muscle mass by conducting a phylogenetic ANCOVA (SVL as covariate, ecomorph as factor). First, 1000 Monte Carlo simulations of character evolution along the branches of the phylogenetic tree were performed for each trait separately (PDSIMUL; Garland et al. 1993). Subsequently, ANCOVAs on the 1000 simulated datasets were carried out, and a ''phylogenetic'' null distribution of $F$-values was created per trait (PDANOVA; Garland et al. 1993). If the $F$-values obtained from ''traditional'' ANCOVAs were greater than the phylogenetic $F$-values at the 0.05 level, differences among ecomorphs were considered statistically significant.

We only report the statistics for the variables mentiaoned above, because previous studies have already documented significant differences in sprint speed and limb length among ecomorphs (see Losos 1990; Irschick and Losos 1998; Losos et al. 1998; Beuttell and Losos 1999).

Since some ecomorph groups only consisted of one species, we were unable to test for differences in slopes among the groups. We only report significance results for the differences among ecomorphs after correcting for differences in SVL (i.e., differences in intercepts).

### *Performance and morphology relationships*

Independent contrasts (IC) for all morphological and performance variables were calculated using the PDTREE program (Garland et al. 1999). General linear models (GLM) do not include an intercept; regressions are forced through the origin (see Garland et al. 1999).

To test for the existence of a trade-off between sprint speed and acceleration capacity, we first regressed the IC of acceleration capacity and sprint speed against the IC of SVL and calculated the residuals. Subsequently, we regressed the residual IC of acceleration capacity against the residual IC of sprint speed. This analysis was done once with the sprint speed data for 16 species collected in this study and validated with the sprint speed data on 12 species collected by Losos (1990).

To test whether the variation in size (SVL) is correlated to the variation in acceleration capacity and/or sprint speed, we regressed the IC of each performance trait against the IC of SVL. Subsequently, we regressed the IC of all morphological variables, except SVL, against the IC of SVL and calculated the residuals.

To test which of the shape variables (i.e., residuals) best explain the variation in acceleration and sprint speed, we performed two sets of analyses. Using GLM, we compared Akaike information criteria (AIC) and log-likelihoods (LL) of different models and tested whether one model performed better than the other. We subsequently performed a multiple regression analysis in which all the independent variables of the best model were entered to determine the direction of the relationships between performance and morphological traits and to take into account the interaction effect among the different independent variables.

For acceleration capacity, we computed two models. In the first, we entered all morphological variables as covariates. Because muscle mass is believed to be of prime importance for determining acceleration capacity (see Delecluse 1997; Curtin et al. 2005), we only included femur retractor mass, knee extensor mass, and ankle extensor mass in the second model. Since both models performed equally well (see below), and, in addition, statistical power decreases with increasing number of predictors (cf. Dunlap et al. 2004), we subsequently performed a multiple regression with the variation in residual IC of acceleration capacity as dependent variable and the residual IC of the three muscle masses as independent variables only.

For sprint speed, we only computed one model. Since both limb segment length and muscle mass are predicted to be important correlates of sprint capacity, we included all morphological variables in this model. We subsequently performed a multiple regression with the residual IC of sprint speed as dependent variable and the residual IC of all six morphological variables as independent variables.

Since our estimates of maximal acceleration capacity are based on the double differentiation of displacement data, whereas our estimates of maximal sprint speed are averages over a given distance, the former may be more variable compared to the latter. To make sure the results from the regression analyses are actually based on biological reality rather than on this kind of methodological artifact, we performed a power analysis. We used a Visual Fortran program written by Dunlap et al. (2004) to calculate the statistical power, that is, the probability of correctly rejecting the null hypothesis of no significant relationship, of both multiple regression models.

## RESULTS

### *Ecomorph Differences*

Descriptive statistics of SVL, femur, tibia, and metatarsus length, femur retractor, knee extensor, and ankle extensor mass are given per species in Appendix 1; descriptive statistics on acceleration and sprint speed per species are presented in Appendix 2.

When comparing the $F$-statistics from the one-way ANCOVAs (SVL as covariate, ecomorph as factor) to the phylogenetic $F$-distributions obtained by 1000 simulations along the phylogenetic tree, we found that the traditional $F$-values were greater than the phylogenetic $F$-values at the 0.05 significance level for acceleration capacity, and the muscle masses of knee and ankle extensors (all three $F_{\text{trad}} > 6.23$; all three $F_{\text{phyl}} < 4.46$). Traditional $F$-values for the femur retractor muscle mass, however, were lower than the phylogenetic $F$-values ($F_{\text{trad}} = 1.38$; $F_{\text{phyl}} = 4.10$). Thus, after correcting for differences in SVL, acceleration capacity and knee and ankle extensor muscle mass differ significantly

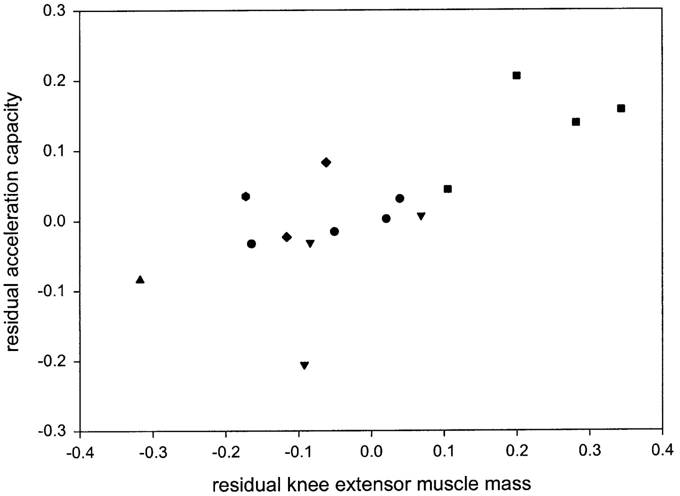

FIG. 2. Plot of residual acceleration versus residual knee extensor muscle mass for 15 *Anolis* lizard species (nonphylogenetically corrected data). Relative acceleration capacity and knee extensor muscle mass coevolved (independent contrasts; see text for details). Symbols refer to six ecomorphs (●, trunk-crown; ■, trunk-ground; ⬣, trunk; ◆, grass-bush; ▲, twig; ▼, crown-giant).

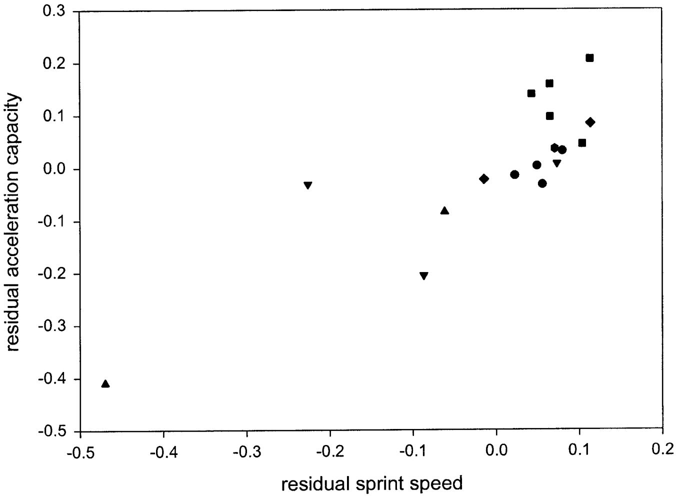

FIG. 3. Plot of residual acceleration versus residual sprint speed for all species used in the analyses (nonphylogenetically corrected). Relative acceleration capacity and sprint speed coevolved (independent contrasts; see text for details). Symbols refer to six ecomorphs (●, trunk-crown; ■, trunk-ground; ⬣, trunk; ◆, grass-bush; ▲, twig; ▼, crown-giant).

among ecomorphs; trunk-ground anoles excel at accelerating and possess the most massive knee and ankle extensors. Twig anoles represent the other extreme, and the rest of the ecomorphs (crown-giant, trunk-crown, trunk, and grass-bush) attain accelerations and have extensor muscle masses in between those two groups (see also Fig. 2).

### *Performance and Morphology Relationships*

Residual IC of acceleration capacity and residual IC of sprint speed correlated positively ($r = 0.79$, $F_{1,15} = 25.33$, $P < 0.0001$). This result is validated using the sprint speed data from Losos (1990) on 12 of the 16 *Anolis* species under study here ($r = 0.80$, $F_{1,10} = 18.09$, $P = 0.002$). A plot of the residual values of the nonphylogenetically corrected acceleration and our sprint speed data of 16 *Anolis* species and two *A. cristatellus* populations is shown in Figure 3. However, the regression of IC of acceleration capacity against IC of SVL was significant and negative ($r = -0.56$, $F_{1,13} = 5.91$, $P = 0.03$), whereas the regression of IC of sprint speed against the IC of SVL was marginally nonsignificant but tended to be positive ($r = 0.49$, $F_{1,13} = 4.07$, $P = 0.065$).

For the residual IC of acceleration capacity, comparing the AIC and LL of the model including the residual IC of all morphological variables with the AIC and LL of the model only including the residual IC of the muscle masses (see Table 1) showed no significant difference in how well either model fits the data (difference in LL = 3.249, df = 3, $P = 0.35$). This result suggests that a model with only muscle masses performs equally well compared to a model with all morphological variables. A multiple regression analysis with residual IC of acceleration capacity as dependent variable and the residual IC of the three muscle masses as independent variables resulted in a significant model ($r = 0.90$, $F_{3,11} = 15.22$, $P < 0.0001$). The statistical power of the acceleration regression model is high (power = 0.89). Of the independent variables, the variation in residual IC of knee extensor muscle mass was the only significant predictor of the variation in the residual IC of acceleration capacity (Table 2; Fig. 2).

The AIC and LL of the model including the residual IC of sprint speed as dependent variable and the residual IC of all six morphological variables as covariates are given in Table 1. A multiple regression with the residual IC of sprint speed as dependent variable and the residual IC of the limb segment lengths and muscle masses as independent variables

TABLE 1. Results from the GLM analyses with the residual IC of acceleration capacity and sprint speed as dependent variable, respectively. Models do not include an intercept. Both acceleration models fit the data equally well ($P = 0.35$). AIC, Akaike information criteria; LL, log likelihoods.

| | AIC | LL | No. of parameters |
|---|---|---|---|
| Acceleration covariates | | | |
| Femur length, tibia length, metatarsus length, femur retractor mass, knee extensor mass, ankle extensor mass | −103.132 | −105.132 | 7 |
| Femur retractor mass, knee extensor mass, ankle extensor mass | −99.883 | −101.883 | 3 |
| Sprint speed covariates | | | |
| Femur length, tibia length, metatarsus length, femur retractor mass, knee extensor mass, ankle extensor mass | −103.897 | −105.897 | 7 |

TABLE 2. Beta, partial correlations, *t*-values and significance levels of the residual independent contrasts (IC) of the different morphological variables in the multiple regressions with the residual IC of acceleration capacity and sprint speed as dependent variable. Both regressions are forced through the origin. In the acceleration model, of the three independent variables, only the variation in residual IC of knee extensor muscle mass explains a significant proportion of the variation in the residual IC of acceleration capacity. In the speed model, the variation in the residual IC of femur length, tibia length, metatarsus length, and knee extensor muscle mass is significantly correlated to the variation in the residual IC of sprint speed.

| | Beta | $r_{\text{part}}$ | $t$ | $P$ |
|---|---|---|---|---|
| Acceleration independent | | | | |
| Femur retractor mass | −0.24 | −0.32 | −1.11 | 0.29 |
| Knee extensor mass | 1.30 | 0.77 | 4.00 | 0.002 |
| Ankle extensor mass | −0.32 | −0.24 | −0.83 | 0.43 |
| Sprint speed independent | | | | |
| Femur length | −1.04 | −0.62 | −2.21 | 0.058 |
| Tibia length | 2.03 | 0.79 | 3.58 | 0.007 |
| Metatarsus length | −1.12 | −0.67 | −2.58 | 0.032 |
| Femur retractor mass | 0.27 | 0.28 | 0.83 | 0.43 |
| Knee extensor mass | 1.15 | 0.55 | 1.88 | 0.098 |
| Ankle extensor mass | −0.81 | −0.49 | −1.60 | 0.15 |

resulted in a significant model ($r = 0.88$, $F_{6,8} = 4.47$, $P = 0.029$). Of the six morphological variables, the variations in the residual IC of femur length, tibia length, metatarsus length, and knee extensor muscle mass were significant predictors of the variation in the residual IC of sprint speed (Table 2). The statistical power of the sprint speed model is 0.55.

## DISCUSSION

Our goal was to investigate how sprint speed and acceleration capacity are intercorrelated and to test which underlying morphological features correlate with both performance traits. Among the 16 species of *Anolis* studied here, we found that relative sprint speed and relative acceleration capacity coevolved and that evolution toward a high sprint capacity has been paralleled by evolution toward a high acceleration capacity. Similar results are found when comparing ecomorphs: trunk-ground anoles are the best accelerators and generally attain the highest sprint speeds (Losos 1990; Irschick and Losos 1999), whereas twig anoles represent the other extreme (Losos 1990; Irschick and Losos 1999; see Fig. 2).

### *Effect of Body Shape*

Of the morphological traits measured, the variation in relative knee extensor mass seems to be the main predictor of the variation in relative acceleration capacity. Similarly, in human athletes faster acceleration requires more muscle mass (Delecluse 1997). In our lizards the knee extensors are also the most important muscle group when it comes to relative sprint speed. The variation in muscle mass of both other functional groups, the femur retractors and ankle extensors, does not explain a significant proportion of the variation in either acceleration or sprint performance across species. To date, only preliminary data on the differential muscle function of 11 limb muscles in a generalized terrestrial lizard, *Sceloporus clarkii*, running at a constant speed is available (Reilly 1995). In *S. clarkii*, the muscles associated with limb retraction, knee extension, and plantar flexion all contribute to the generation of force during running (Reilly 1995). However, kinematic data over a relatively narrow range of speeds in the same species suggest that femur retraction, and thus the caudofemoralis muscle, is the primary component producing propulsive force (Reilly and Delancey 1997; see also Nelson and Jayne 2001). Although this is likely true for *Anolis* lizards as well, our comparative data do suggest a more important role for the knee extensors in attaining high acceleration and sprint performance. Moreover, Snyder (1954) concluded, based on comparative myology of four iguanid and two agamid lizard species, that the femorotibialis muscle, a knee extensor, does provide a large part of the propulsive force that moves the body upward and forward. In addition, in humans, the gluteus maximus, a femur retractor, and the knee extensors are the main accelerators (Delecluse 1997).

Also, contrary to locomotion on a flat surface (cf. Reilly 1995; Reilly and Delancey 1997; Nelson and Jayne 2001), the caudofemoralis muscle might not be able to contribute extensively to overall propulsion on a dowel because the movement of the femur itself is constrained by the curved surface. When running on a dowel, limb posture is less sprawled than on a flat surface and overall femur retraction is reduced (see Spezzano and Jayne 2004). Similarly, the ankle extensor muscles might be less important in generating high propulsive forces on round surfaces (and thus not determine locomotor performance). As the orientation of the surface from which the foot pushes off becomes more curved, the foot is prevented from rolling off, and the overall contribution of ankle extension to propulsion is smaller (Spezzano and Jayne 2004).

In addition, a plausible explanation is that the mass of some muscles is constrained by physical space requirements, whereas the mass of others is not, or to a lesser degree. The primary contributor to the femur retractor group is the caudofemoralis muscle, originating on the first five to seven caudal vertebrae and inserting on the proximal aspect of the femur (see e.g., Nelson and Jayne 2001; A. Herrel and B. Vanhooydonck, pers. obs.). As in most other lizards, anoles are known to use caudal autotomy as part of a predator escape response (A. Herrel and B. Vanhooydonck, pers. obs.). However, the point at which the tail breaks depends on the place of origin of the caudofemoralis muscle. Zani (1996) showed that the evolution of the caudofemoralis length negatively influences caudal autotomy evolution in lizards, thus indicating that the caudofemoralis muscle cannot elongate in caudal direction without decreasing the ability to lose the tail (Zani 1996; Russell et al. 2001). The knee extensors, on the contrary, do not seem constrained in this manner, and increases in length and/or volume are theoretically possible without impairment of other functions. This idea is substantiated by the fact that the interspecific variation in relative knee extensor muscle mass is greater than the variation in relative femur retractor mass. Moreover, ecomorphs differ significantly in the former and not in the latter (see Appendix 1).

Relative sprint speed, in addition to being correlated to the variation in knee extensor muscle mass, covaries with femur, tibia, and metatarsus length among anoles. Previous studies have repeatedly shown that long limbs are advantageous for attaining high sprint speeds, because they represent ''high-gear'' systems and thus increase stride length (e.g., Hildebrand 1985; Garland and Losos 1994; Irschick and Jayne 1998; Vanhooydonck et al. 2002). Likewise, a positive relationship between hind limb length and speed has been previously reported among *Anolis* lizard species (e.g., Losos and Sinervo 1989; Losos 1990). In addition, our analyses suggest that the elongation of the hind limb is primarily due to changes in tibia length, since for a given tibia, femur and metatarsus length appear to be negatively correlated to sprint speed. The overall contribution of the femur and metatarsus to locomotor performance on a dowel thus appears limited in comparison to that of the tibia (Spezzano and Jayne 2004).

Our results thus indicate that the functional traits required to excel in either performance trait partly overlap, potentially explaining the positive correlation between the variation in relative sprint speed and acceleration capacity among *Anolis* lizards. Whereas the variation in acceleration capacity seems primarily correlated to the variation in the muscle mass of the knee extensors, the variation in sprint speed is correlated to the variation in both limb length and muscle mass. Interestingly, our results suggest that acceleration capacity might represent a case of one-to-one mapping of form and function, at least with regard to the morphological variables studied here, whereas similar sprint speeds can be achieved through various combinations of limb segment lengths and knee extensor muscle mass. Sprint speed in *Anolis* lizards thus clearly represents a case of redundant or many-to-one mapping (Alfaro et al. 2004, 2005; Wainwright et al. 2005). Similarly, *Anolis* jumping ability is also determined by different combinations of limb and muscle traits (Toro et al. 2004). Since knee extensor muscle mass affects both sprint speed and acceleration capacity in the same way, all else being equal, an increase in knee extensor muscle mass will lead to an increase in both acceleration capacity and sprint speed. Sprint speed, on the contrary, could further increase due to changes in limb segment length while keeping knee extensor muscle mass constant. Thus, although both performance measures in our sample of *Anolis* species appear to be tightly linked, the fact that similar sprint speeds can be achieved through various combinations of limb segment lengths and muscle mass whereas acceleration capacity is mainly affected by muscle morphology could, in theory, result in a partial decoupling between speed and acceleration. Data on speed and acceleration capacity in other groups are needed to test this idea further.

### *Effect of Body Size*

Based on theoretical models and some empirical studies, we hypothesized that body size might may have an opposing effect on speed and acceleration. Although sprint speed has been shown to be positively correlated to size (see Garland and Losos 1994; Van Damme and Vanhooydonck 2001), Hill (1950) predicted that acceleration capacity is negatively affected by size. Our data corroborate these ideas. Whereas the variation in body size is negatively correlated to the variation in absolute acceleration capacity in *Anolis* lizards, the opposite tends to be true for sprint speed. The latter relationship exists at both the intra- and interspecific level in squamates (see reviews in Garland and Losos 1994; Van Damme and Vanhooydonck 2001). However, the effect of body size on acceleration capacity in terrestrial vertebrates has remained equivocal. (e.g., Huey and Hertz 1984; Carrier 1995; Wilson et al. 2000, Toro et al. 2003), although Hill (1950) predicted that acceleration capacity should decline with body size because mass scales with length to the third power, whereas muscular force scales with length to the second. Interestingly, the outcome of the empirical studies seems to depend heavily on which size range or age class is compared. In all cases (except Huey and Hertz 1984), acceleration capacity scales positively within smaller individuals, whereas it scales negatively in larger individuals (e.g., juvenile vs. adult jackrabbits, metamorphic vs. postmetamorphic frogs, *Anolis carolinensis* and *A. sagrei* vs. crown-giants, *A. garmani* and *A. equestris*; Carrier 1995; Wilson et al. 2000; Toro et al. 2003). Although these examples represent take-off acceleration when hopping or jumping, the same pattern emerges when examining our running data, although it seems to be largely driven through the inclusion of the smallest *Anolis* species, *A. occultus*, in our sample (see Fig. 4). Carrier (1983, 1995) explained the differential scaling of body size and acceleration capacity in jackrabbits by a greater mechanical advantage around the joints and stronger muscles in young hares compared to adults, resulting in a greater force production relative to body size. Accordingly, young hares are able to accelerate more quickly than adults (Carrier 1983, 1995). Since we lack detailed comparative musculoskeletal data, it is unclear whether the same explanation holds at an interspecific level and when performing a mechanically different locomotor task such as running.

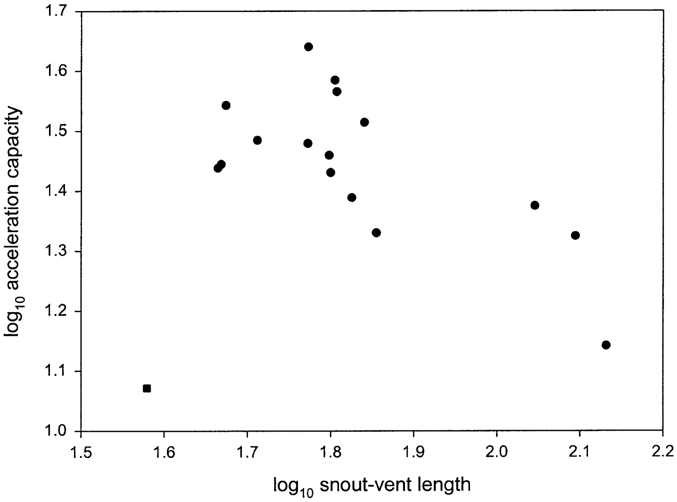

FIG. 4. Plot of logarithmically transformed acceleration capacity versus snout-vent length. When comparing 15 species for which all morphological data was available (see text for details) acceleration capacity and body size are negatively correlated. *Anolis occultus* (■), however, is the smallest and the worst accelerator.

In summary, we found that sprint speed and acceleration capacity are positively correlated across 16 species of *Anolis* lizards. Moreover, the variation in acceleration capacity is correlated to the variation in knee extensor muscle mass, whereas the variation in sprint speed is correlated to both the variation in muscle mass and limb segment lengths. Our findings support recent theoretical work showing that the same function can be achieved through several different pathways (Alfaro et al. 2004, 2005; Wainwright et al. 2005). Hence, our work supports the general notion that organisms may exhibit more functional flexibility than previously thought.

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## APPENDIX 1

Means and standard errors per species of snout-vent length (SVL), limb segment lengths, and muscle masses of the three functional muscle groups. Numbers of individuals measured and dissected per species are provided. Eco indicates to which ecomorph each species is assigned (cf. Beuttell and Losos 1999): TW, twig; CG, crown-giant; GB, grass-bush; TG, trunk-ground; TC, trunk-crown; TR, trunk.

| | | Morphometry (mm) | | | | | Muscle mass (mg) | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Eco | *n* | SVL | Femur | Tibia | Metatarsus | *n* | Femur retractors | Knee extensors* | Ankle extensors* |
| *A. occultus* | TW | 2 | 37.95 ± 0.3 | 5.88 ± 0.20 | 5.09 ± 0.15 | 2.61 ± 0.18 | | | | |
| *A. equestris* | CG | 9 | 135.40 ± 11.16 | 28.55 ± 2.31 | 25.91 ± 1.92 | 14.79 ± 1.16 | 2 | 1044.85 ± 117.69 | 495.75 ± 12.62 | 373.06 ± 28.68 |
| *A. cuvieri* | CG | 15 | 124.33 ± 2.06 | 34.20 ± 0.76 | 28.32 ± 0.49 | 16.05 ± 0.27 | 1 | 370.23 | 283.09 | 171.62 |
| *A. krugi* | GB | 18 | 47.19 ± 0.45 | 12.21 ± 0.14 | 11.36 ± 0.12 | 5.94 ± 0.14 | 2 | 25.08 ± 5.34 | 18.26 ± 3.04 | 8.30 ± 1.89 |
| *A. pulchellus* | GB | 17 | 46.15 ± 0.43 | 10.45 ± 0.15 | 9.95 ± 0.15 | 5.30 ± 0.13 | 2 | 41.01 ± 1.96 | 22.07 ± 0.06 | 12.51 ± 0.97 |
| *A. gundlachi* | TG | 16 | 64.17 ± 0.89 | 17.97 ± 0.21 | 16.41 ± 0.22 | 9.40 ± 0.12 | 3 | 108.30 ± 11.28 | 146.59 ± 16.25 | 61.74 ± 2.91 |
| *A. cristatellus* (PR) | TG | 17 | 69.25 ± 0.79 | 18.14 ± 0.25 | 16.83 ± 0.28 | 9.16 ± 0.16 | | | | |
| *A. cristatellus* (FL) | TG | 5 | 63.84 ± 3.06 | 15.93 ± 1.10 | 15.07 ± 0.78 | 8.77 ± 0.69 | 3 | 188.13 ± 21.14 | 164.78 ± 22.37 | 88.58 ± 7.35 |
| *A. evermanni* | TC | 15 | 63.07 ± 1.16 | 15.67 ± 0.29 | 14.19 ± 0.20 | 7.67 ± 0.17 | 3 | 100.54 ± 2.13 | 65.89 ± 3.41 | 34.60 ± 0.61 |
| *A. stratulus* | TC | 22 | 46.58 ± 0.32 | 10.76 ± 0.12 | 10.07 ± 0.12 | 5.51 ± 0.08 | 3 | 36.12 ± 4.67 | 26.73 ± 4.18 | 12.94 ± 1.67 |
| *A. distichus* | TR | 4 | 51.48 ± 0.70 | 11.61 ± 0.23 | 12.21 ± 0.21 | 6.54 ± 0.16 | 3 | 37.89 ± 12.18 | 23.94 ± 7.44 | 12.8 ± 4.89 |
| *A. grahami* | TC | 4 | 62.81 ± 0.92 | 15.09 ± 0.63 | 14.14 ± 0.39 | 7.58 ± 0.51 | 3 | 132.22 ± 17.62 | 70.35 ± 15.02 | 38.52 ± 7.52 |
| *A. garmani* | CG | 7 | 111.07 ± 2.53 | 24.99 ± 0.83 | 24.64 ± 0.42 | 13.16 ± 0.28 | 1 | 537.26 | 328.55 | 187.8 |
| *A. lineatopus* | TG | 10 | 59.31 ± 0.82 | 15.54 ± 0.27 | 14.52 ± 0.21 | 7.76 ± 0.19 | 1 | 100.93 | 95.78 | 49.87 |
| *A. valencienni* | TW | 7 | 71.62 ± 1.33 | 12.72 ± 0.29 | 11.83 ± 0.23 | 6.93 ± 0.13 | 2 | 97.33 ± 7.05 | 38.77 ± 5.78 | 22.88 ± 8.01 |
| *A. sagrei* | TG | 19 | 59.20 ± 0.34 | 13.60 ± 0.13 | 13.14 ± 0.07 | 6.46 ± 0.09 | 2 | 99.38 ± 13.87 | 62.12 ± 16.19 | 64.26 ± 26.71 |
| *A. carolinensis* | TC | 16 | 66.90 ± 0.44 | 13.71 ± 0.12 | 12.34 ± 0.12 | 5.71 ± 0.12 | 3 | 132.56 ± 7.77 | 57.33 ± 1.24 | 32.55 ± 3.36 |

* Differences among ecomorphs are significant (phylogenetic ANCOVA, $P < 0.05$).

## APPENDIX 2

Means and standard errors per species of locomotor performance. Number of individuals measured and observed per species is shown. Eco indicates to which ecomorph each species is assigned (cf. Beuttell and Losos 1999): TW, twig; CG, crown-giant; GB, grass-bush; TG, trunk-ground; TC, trunk-crown; TR, trunk.

| Species | Eco | *n* | Acceleration ($\mathrm{m\ sec^{-2}}$)* | Sprint speed ($\mathrm{m\ sec^{-1}}$) |
|---|---|---|---|---|
| *A. occultus*[1] | TW | 3 | 11.79 ± 3.43 | 0.25 ± 0.01 |
| *A. equestris* | CG | 6 | 13.84 ± 1.60 | 1.29 ± 0.10 |
| *A. cuvieri* | CG | 16 | 21.12 ± 2.18 | 0.89 ± 0.07 |
| *A. krugi* | GB | 18 | 34.87 ± 1.80 | 1.11 ± 0.05 |
| *A. pulchellus* | GB | 17 | 27.43 ± 1.98 | 0.81 ± 0.05 |
| *A. gundlachi* | TG | 22 | 36.76 ± 2.77 | 1.12 ± 0.08 |
| *A. cristatellus* (PR) | TG | 17 | 32.66 ± 2.36 | 1.24 ± 0.06 |
| *A. cristatellus* (FL) | TG | 9 | 38.42 ± 4.12 | 1.18 ± 0.10 |
| *A. evermanni* | TC | 16 | 26.96 ± 2.12 | 1.13 ± 0.05 |
| *A. stratulus* | TC | 25 | 27.84 ± 1.27 | 0.89 ± 0.04 |
| *A. distichus* | TR | 14 | 30.53 ± 2.42 | 1.05 ± 0.06 |
| *A. grahami* | TC | 12 | 28.81 ± 2.59 | 1.21 ± 0.08 |
| *A. garmani* | CG | 8 | 23.72 ± 3.45 | 1.66 ± 0.10 |
| *A. lineatopus* | TG | 14 | 43.66 ± 2.53 | 1.26 ± 0.05 |
| *A. valencienni* | TW | 10 | 21.38 ± 2.24 | 0.94 ± 0.07 |
| *A. sagrei* | TG | 21 | 30.15 ± 1.93 | 1.23 ± 0.06 |
| *A. carolinensis* | TC | 15 | 24.49 ± 1.99 | 1.19 ± 0.04 |

[1] Sprint speed measured over 0.10 m and $n = 2$.

* Differences among ecomorphs are significant (phylogenetic ANCOVA, $P < 0.05$).