

Intraspecific correlations among morphology, performance and habitat use within a green anole lizard (*Anolis carolinensis*) population

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We examined habitat use, morphology, jumping and clinging ability for 403 juvenile, female and male green anole lizards, *Anolis carolinensis*, in a population in south-eastern Louisiana. We sought to answer three questions: (1) Do age/sex classes differ in habitat use, morphology and performance ability? (2) Do habitat use, morphology and performance correlate among all individuals across three age/sex classes (juveniles, females and males)? (3) Do juveniles compensate for their poor absolute performance capacities by being better performers on a relative scale? The three age/sex classes were found to differ significantly in size-adjusted morphology, habitat use and size-adjusted performance capacity. Juveniles tended to occupy perches which were closer together than those of adult males and females. The distal elements of the hindlimb (femur, tibia) were significantly longer in males than in females and juveniles, while females were more stocky than males and juveniles. The only significant overall ecomorphological relationship detected was between the lengths of the distal hindlimb elements and maximum jump acceleration. Our hypothesis that juveniles should be better performers (relative to size) compared to adults was disproved, as adult females were always the best performers relative to size. Our analysis of a mainland anole population presents a different view of population structure compared to similar studies involving Caribbean *Anolis* lizards, which show more ecological differentiation among age/sex classes, and also show that juveniles are relatively good performers. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, 85, 211–221.

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INTRODUCTION

A key issue in ecology concerns how morphological, ecological and functional capacities are related, both among different species, and among individuals of different sexes and sizes within a single population or species (Lauder, 1990; Losos, 1990; Wainwright, Osenberg & Mittelbach, 1991; Carrier, 1996). Interspecific ecomorphological studies typically assume that significant relationships between ecology and morphology provide evidence of adaptation (Karr & James, 1975; Miles & Ricklefs, 1984; Miles, Ricklefs & Travis, 1987;

Winemiller, 1991; Irschick *et al.*, 1997; see also Wainwright & Reilly, 1994 and references therein). Within a species, however, ecomorphological correlations are more difficult to interpret, and may also reflect adaptations by different intraspecific classes (i.e. adult males, adult females, and juveniles; Werner & Gillam, 1984; Carrier, 1996).

Over the past 15 years, researchers have emphasized the importance of incorporating functional measures within ecomorphological studies (Wainwright, 1994; Irschick, 2002). Within a species, researchers have most often followed the paradigm in which morphological variation is presumed to translate into variation in performance capacity, which ultimately translates into variation in fitness among individuals

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(Arnold, 1983; Emerson & Arnold, 1989; Vanhooydonck & Van Damme, 2001; Vanhooydonck, Van Damme & Aerts, 2001). However, relatively few studies have simultaneously examined relationships among morphology, habitat use and performance among individuals of a single species, although doing so could shed a significant amount of light on why different age and sex classes frequently differ in habitat use (Werner & Gillam, 1984). For example, if one age/sex class, for example juveniles, performs particularly poorly for some important capacity (e.g. maximum speed), then it might be expected to occupy a habitat in which the risk of predation is relatively low (e.g. more cluttered as opposed to more open).

Two key (and often interrelated) variables that can affect performance, and hence habitat use, are size and sex (e.g. Werner & Gillam, 1984; Adolph, 1990; Wainwright *et al.*, 1991; Martin & Lopez, 1995; Carrier, 1996; Herrel *et al.*, 2005). One recurring finding is that increased size within a species often results in enhanced performance (e.g. squamates, see Garland & Losos, 1994), particularly on an absolute scale (e.g. maximum jump distance), although it is unclear whether, for many performance variables, relative (size-adjusted) or absolute values of performance are more ecologically relevant (Van Damme & Van Doren, 1999). Similarly, adult males and females often differ in various performance capacities, although it is sometimes unclear whether such differences are due to variation in size (as males are often larger), or some other sex-based physiological differences (e.g. hormonal).

Differences in either absolute or relative performance capacities among age/sex classes might also be correlated with differences in morphological shape. For example, if juveniles have relatively long limbs for their size (compared to larger males), then they might be expected to jump further or sprint faster on a relative scale, hence partially compensating for their poor absolute performance capacities (Carrier, 1996; Irschick, 2000; Herrel *et al.*, 2005). Thus, simultaneously studying habitat use, ecologically relevant performance capacities and morphological shape in different intraspecific classes may reveal important aspects of how they cope with the constraining effects of size.

Squamates (lizards and snakes) are excellent subjects for investigating these issues because, unlike mammals or birds, juveniles are typically born with fully developed motor skills for important activities such as running, jumping or biting (Carrier, 1996). Furthermore, because of the general lack of parental care, they are often under intense selective pressure from predators, including larger individuals of their own species. Thus, one might predict that selection would favour high levels of relative (size-adjusted) performance.

We addressed these issues by examining habitat use, two kinds of performance (jumping ability and clinging), and morphology in juveniles, adult females and adult males of the green anole, *A. carolinensis*, within a freshwater swamp population in Louisiana. We asked three primary questions: (1) Do the three age/sex classes differ in habitat use, morphology and performance ability? (2) Do habitat use, morphology and performance correlate among all individuals across the three age/sex classes? (3) Do juveniles compensate for their poor absolute performance capacities by being better performers on a relative scale?

MATERIAL AND METHODS

HABITAT SAMPLED

Lizards ($N = 403$) were sampled from vegetation along a 755 m transect that follows a straight dirt road which crosses Good Hope Field in St. Charles Parish, south-eastern Louisiana (29.91°N, 90.36°W). This transect consists of a rarely used dirt access road is bordered on both sides by relatively narrow strips of vegetation (each about 3–4 m wide). It passes through the middle of an open-water swamp, which effectively blocks the movement of lizards except up and down the transect. The vegetation is a mixture of low-lying shrubs and grass interspersed with larger trees and bushes.

MEASUREMENTS OF RANDOM AND ACTUAL HABITAT USE

All fieldwork took place between 1 September and 30 October 2002. The availability of structural habitat for *A. carolinensis* was quantified within the transect by measuring the availability of perches at 1 and 2 m (relatively few lizards perched above 2 m, see Results) at regular intervals along the transect. 2-m-long rods were placed parallel to the ground, and perpendicular to the transect, at heights of 1 and 2 m, with their centre points located *c.* 250 cm away from the road (and thus roughly in the middle of the strips of vegetation). Any perches that were within 5 cm of the rods were measured.

We defined a perch as any surface in between two nodes. For each perch, we measured its diameter, length, distance to the nearest perch (D_{np} , taken from the middle of each perch), and diameter of that closest perch (PD_{np}). The transect was sampled every 20 m, alternately on the left and right sides, providing a total of 38 sample points. In addition, at each sampling point, we measured the distance from the edge of the road to the edge of the water (mean = 3.45 ± 1.09 m [SD]), and from this mean value, and the total transect length of 755 m, we estimated the total habitat area sampled as 5285 m².

To determine the actual habitat use of anoles, we walked along the transect daily when lizards were active (09.00 to 17:00 h), and captured any lizard sighted. We recorded the following variables for each lizard upon capture: substrate type (e.g. tree trunk, branch) perch height, diameter and length, D_{np} and PD_{np} . The position of each lizard was marked using a GPS unit and with coloured flags, and after performance trials were completed, the animal was returned to its original point of capture (typically within 48 h). We attempted to sample evenly by walking the entire transect each day, except when there was torrential rain.

PERFORMANCE MEASUREMENTS

For all individuals, two kinds of performance were measured: maximum jumping capacity and maximum clinging capacity. Lizards were housed in 10-gallon aquaria overnight and misted with water to prevent dehydration. They were allowed to rest both between different trials of a particular kind of performance and for at least 2–3 h between tests of different kinds of performance. All individuals were placed inside an incubator at 32 °C (similar to their preferred field temperature) for at least 1 h prior to testing.

Jumping capacity

We used a custom-designed force plate (30 cm long \times 18 cm wide \times 1 cm high) to measure the 3-dimensional ground reaction forces during jumping (see Heglund, 1981 and Toro *et al.*, 2003 for a detailed description of methods used). We attempted to obtain at least five good jumps for each lizard based upon three trials. The 'best' jump for each individual was judged to be that with the longest horizontal distance. Because anoles jump readily, we did not have difficulty eliciting maximal performance from each individual. For this analysis, we focused on three key variables that are likely to have ecological significance for these lizards: maximum jump distance, velocity, and acceleration.

Clinging ability

This was measured by inducing lizards to adhere to an acetate sheet attached to the surface of the force plate with tape (for methods see Elstrott & Irschick, 2004). Because the substrate was smooth, our measure of clinging ability did not include the claws of the lizards. Each lizard participated in a session consisting of three trials, with approximately an hour of rest between each one.

During a trial, the lizard was removed from the incubator and placed with its front feet on the acetate sheet (see below). It was then repeatedly dragged horizontally at a constant speed (i.e. not jerked) across the

force plate for 30 s. We estimated the pulling speed to be approximately 5 cm/s. Only one investigator (DJI) conducted these trials to ensure consistency. Slight differences in the velocity of dragging did not affect force output, although rapid acceleration can potentially affect it (Autumn, unpubl. data). The lizard was returned to the incubator, and the top five performances recorded for that trial. We only included trials in which lizards exerted maximum effort by extending both forelimbs and placing their toepads flush on the sheet. Not all of the 403 lizards examined provided a satisfactory measure of clinging ability ($N = 217$; 134 adult males, 45 adult females, 38 juveniles).

MORPHOLOGICAL VARIABLES

The following morphological variables were measured for each individual: mass, snout–vent length (SVL), and the lengths of the tail, humerus, radius, metatarsus of the forelimb, longest toe of the forelimb, femur, tibia, and longest toe of the hindlimb. The images of both sets of forelimb toepads were digitized using an HP Scanjet 5370C and saved as JPEG files. Their combined areas were calculated using the program TpsDig. Mass was recorded by placing the lizards inside a small cup on a Denver instruments M-220 electronic balance accurate to the nearest 0.01 g.

DATA ANALYSIS

We divided the data into three groups. Juveniles did not appear to be sexually mature and thus did not display any obvious sexual traits (e.g. an enlarged dewlap for males). Adult females were greater than 40 mm SVL; they exhibited a narrow tail base and a reduced dewlap area. Adult males were greater than 45 mm SVL; they exhibited enlarged tail bases and dewlap areas.

To compare random vs. actual patterns of habitat use, we first inspected the actual perch heights of the three age/sex classes, which averaged about 1.5 m for all three (Table 1). Having sampled the habitat at 1 and 2 m, we pooled the random data from these two heights to compare with actual use. We created frequency distributions of each variable (perch diameter and length, D_{np} and PD_{np}) and compared random vs. actual distributions using Kolmogorov–Smirnov tests. Because we were primarily interested in age/sex differences in habitat use, we conducted tests for each class separately.

When comparing habitat use, morphology and performance capacity, we first reduced the number of variables for statistical analysis by conducting principal components analysis (PCA, rotated using varimax) on the habitat and morphological data. For the morphological data set, we used as input residual values of each log-transformed variable after regression

Table 1. Descriptive statistics for random and actual habitat measures for three different sex and age classes of *Anolis carolinensis*. Values are means \pm 1 SE, with median values in parentheses. *Abbreviations:* PH, perch height; PD, perch diameter; PL, perch length; D_{np} , distance to nearest perch; PD_{np} , diameter of nearest perch

	PH	PD	PL	D_{np}	PD_{np}
RANDOM	–	0.8 \pm 0.2 (0.3)	28.8 \pm 2.5 (16.0)	8.4 \pm 0.6 (6.0)	0.7 \pm 0.1 (0.3)
ACTUAL					
Juveniles ($N = 157$)	155.5 \pm 7.0 (154.0)	2.5 \pm 0.6 (0.8)	36.6 \pm 4.4 (20.0)	7.6 \pm 1.0 (5.0)	1.2 \pm 0.3 (0.3)
Adult females ($N = 81$)	149.3 \pm 8.4 (140.5)	5.4 \pm 0.9 (1.6)	95.3 \pm 13.8 (50.0)	9.2 \pm 0.8 (8.0)	2.0 \pm 0.5 (0.3)
Adult males ($N = 220$)	154.7 \pm 4.7 (154.5)	4.0 \pm 0.5 (1.5)	76.9 \pm 6.9 (44.0)	9.2 \pm 0.6 (7.0)	1.3 \pm 0.2 (0.5)

against log-transformed SVL. Because we were primarily interested in habitat differences on an absolute scale (e.g. perch height), we used non-size adjusted values in the habitat PCA. We only included those PCs for which the eigenvalues were greater than 1.0 (see Jackson, 1993). We did not conduct a PCA for the performance variables, because of the smaller number ($N = 4$ variables: max. jump distance, velocity and acceleration, and max. clinging ability).

To address our first question of whether age/sex classes differ in these three aspects (habitat use, morphology and performance), we conducted one-way MANOVAs (using age/sex class as the lone factor, $N = 3$ levels) on the statistically significant PCs for each data set (or for residual values of jumping and clinging variables based on regressions of each log-transformed variable against log-transformed SVL). Because we did not acquire values of clinging ability for all individuals for which we gained jumping data, we chose to analyse the former separately using a one-way ANOVA. Similarly, because toepad area is a distinct morphological variable from the other linear dimensions, we chose to examine differences in area residuals (based on regressions between log-transformed toepad area vs. log-transformed SVL) also using a one-way ANOVA.

To address our second question of whether habitat use, morphology and performance were correlated among all individuals of all age/sex classes, we conducted a canonical correlation analysis (CCA; see Miles & Ricklefs, 1984) using as input residual values for morphology and performance, and non-size-adjusted log-transformed values of habitat use. We used these raw values, rather than PCs, to avoid conducting multivariate analyses on composite variables. All statistical analyses were completed using SYSTAT v. 10.0 for PC.

RESULTS

HABITAT DATA

Anoles primarily occupied branches (68%) and tree trunks (18%), with a smaller number using leaves or

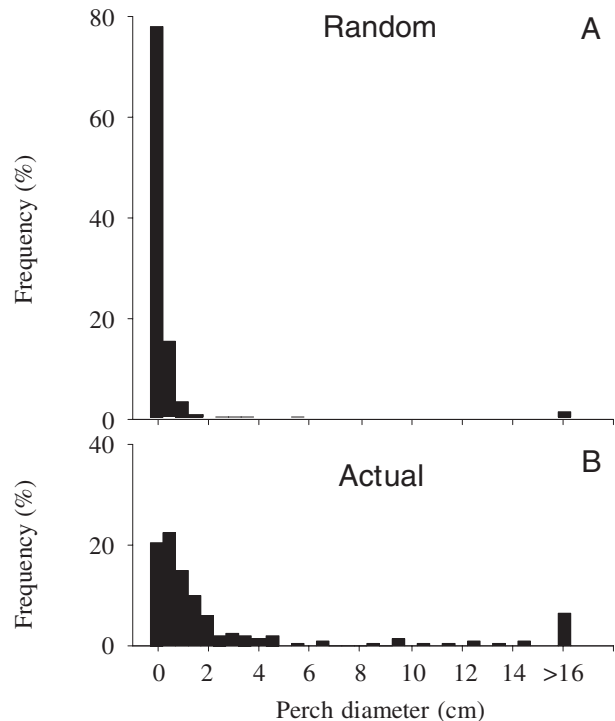


Figure 1. Frequency distributions of perch diameters based on (A) random measures of habitat use, and (B) actual habitat use. B shows perch diameters for all 403 green anoles, thus pooling all three sex/age classes. Note the large diameters at the right of the graph, indicating large trees.

stems of grass (8%), or other surfaces (6%). The random habitat data show that the habitat is dominated by narrow perches of relatively short length, with the vast majority less than 2 cm in diameter. Exceptions included a small group of large trees, where perch diameters were large (Fig. 1, Table 1).

Habitat use of both juveniles and females differed significantly from the random habitat data for all variables excluding perch height (for which there are no random data; Table 2), whereas that of males differed

Table 2. Results from Kolmogorov–Smirnov tests (D_{\max} values) comparing random vs. actual distributions for different ecological variables for each age/sex class of *Anolis carolinensis*. * $P < 0.05$, ** $P < 0.01$. Abbreviations per Table 1

	PD	PL	D_{np}	PD_{np}
Juveniles	0.25*	0.29*	0.32*	0.43**
Adult females	0.37**	0.34*	0.47**	0.70**
Adult males	0.28*	0.27	0.28	0.54**
d.f.	28	22	17	22

Table 3. Loadings of habitat variables in a PCA. Abbreviations per Table 1. All measurements in cm. Substantial loadings are in bold

Variable	PC 1	PC 2	PC 3	PC 4
PH	-0.06	-0.96	-0.13	-0.13
PD	0.21	0.15	0.22	0.91
PL	0.26	0.26	0.21	0.28
D_{np}	0.94	0.06	0.18	0.19
PD_{np}	0.18	0.14	0.94	0.20
% variance explained	20.6	20.8	20.4	19.9

Table 4. Mean (± 1 SE) morphological measures for three different sex and age classes of *Anolis carolinensis*. All measurements (apart from Mass, g) in mm

Variable	Juveniles	Adult females	Adult males
SVL	40.2 \pm 0.65	50.8 \pm 0.66	60.7 \pm 0.46
Mass	1.4 \pm 0.06	2.9 \pm 0.09	4.7 \pm 0.11
Tail length	73.0 \pm 9.59	92.2 \pm 1.58	108.5 \pm 1.01
Femur	7.9 \pm 0.12	9.6 \pm 0.11	11.6 \pm 0.09
Tibia	7.8 \pm 0.12	9.4 \pm 0.10	11.4 \pm 0.08
Metatarsus hindlimb	4.8 \pm 0.08	5.7 \pm 0.06	7.0 \pm 0.05
Longest toe hindlimb	5.6 \pm 0.09	6.5 \pm 0.07	7.8 \pm 0.07
Humerus	6.5 \pm 0.12	8.2 \pm 0.12	10.0 \pm 0.09
Radius	4.7 \pm 0.07	5.7 \pm 0.07	7.0 \pm 0.06
Metatarsus forelimb	1.9 \pm 0.04	2.4 \pm 0.04	2.8 \pm 0.03
Longest toe forelimb	3.3 \pm 0.07	3.7 \pm 0.05	4.5 \pm 0.04

from random only for perch diameter and PD_{np} . All three age/sex classes tended to use relatively broad perches compared to those available in the habitat and also had higher values of PD_{np} compared to the random distribution (Tables 1, 2). Juveniles and females tended to use relatively long perches compared to those available, with the former using perches with significantly shorter values of D_{np} compared to random expectations (Tables 1, 2). All three age/sex classes perched at similar heights, ranging from an average of 149.3 cm (females) to 155.5 cm (juveniles) (Table 1).

The PCA on five habitat variables (Table 3) yielded three primary PCs that together explained about 60% of the variation among individuals, although only the first PC was judged to be meaningful (eigenvalue = 2.79), showing high and positive loadings with the D_{np} .

MORPHOLOGY AND PERFORMANCE

Table 4 provides summary statistics of morphological characteristics for all three age/sex classes. Tail

lengths were not included in the PCA because of the large number of individuals with missing or regenerated tails. PCs 1–3 explained about 33.7% of the variation in morphology, and all had eigenvalues greater than 1.0 (2.18, 1.69, and 1.10, respectively). Because the eigenvalues for the other PCs were less than 1.0, we did not include them in further analysis. PC 1 had a high and positive loading for metatarsal length, PC 2 for mass, and PC 3 for humerus length (Table 5). Toepad area increased significantly with SVL (slope = 1.87 ± 0.04 , $y\text{-int} = -2.17 + 0$, $r^2 = 0.84$, $P < 0.001$), but the classes did not differ significantly in residual toepad area (one-way ANOVA, $F_{2,369} = 0.46$, $P > 0.50$). Table 6 provides summary statistics of all performance measures, while in Figure 2 a representative jumping variable (max. distance, Fig. 2A) and clinging ability (Fig. 2B) are plotted against SVL, respectively.

DIFFERENCES AMONG AGE/SEX CLASSES

As only one PC within the habitat data was statistically significant, we conducted a one-way univariate ANOVA for it, which differed significantly among age/sex classes (Table 7). Females tended to have the high-

est values of PC 1 (mean = 0.27), followed by males (mean = 0.10), and juveniles (mean = -0.45). Because D_{np} loaded highly and positively on PC 1 (see Table 3), females and males tended to have higher values compared to juveniles, which accords with Table 1.

MANOVAs were also statistically significant overall for both morphology ($\lambda = 0.91$), and performance ($\lambda = 0.95$; see Table 7 for F -values). For morphology, PCs 1 and 2 differed significantly among the age/sex classes. Males had the highest values of morphology PC 1 (mean = 0.17), followed by juveniles (mean = -0.09), and females (mean = -0.33). Because PC 1 had high and positive loadings with hindlimb metatarsus length (see Table 5), then males tended to have longer metatarsal hindlimb elements compared to juveniles and females. Females had much higher values for PC 2 (mean = 0.40) compared to juveniles (mean = -0.27) and males (mean = -0.03). Because morphology PC 2 had a high positive loading for mass, this indicates that females had relatively more 'massive' or 'stocky' bodies compared to juveniles or males. As we only examined non-gravid females, these differences cannot be attributed to effects of gravidity.

Residual values of all three jump variables (distance, velocity, and acceleration) differed significantly

Table 5. Loadings of morphological variables in PCA. Substantial loadings are in bold

Variable	PC 1	PC 2	PC 3
Mass	-0.072	0.983	0.002
Femur	0.079	0.058	0.152
Tibia	0.294	0.064	0.147
Metatarsus hindlimb	0.950	-0.010	0.127
Longest toe hindlimb	-0.031	0.078	-0.065
Humerus	0.123	0.011	0.968
Radius	0.013	0.136	-0.035
Metatarsus forelimb	0.021	0.074	-0.047
Longest toe forelimb	-0.060	0.022	0.028
% variance explained	11.3	11.2	11.2

Table 6. Mean (± 1 SE) performance measures for three different sex/age classes of *Anolis carolinensis*. Non-size-adjusted values (mean residual values)

Variable	Juveniles	Adult females	Adult males
CLINGING ABILITY			
Max. cling force (N)	0.60 ± 0.06 (-0.02)	1.72 ± 0.07 (0.05)	2.03 ± 0.06 (-0.01)
JUMPING CAPACITY			
Max. takeoff velocity (m/s)	1.13 ± 0.02 (-0.009)	1.37 ± 0.02 (0.022)	1.43 ± 0.01 (-0.005)
Max. takeoff acceleration (m/s ²)	25.42 ± 0.48 (-0.010)	30.06 ± 0.39 (0.031)	29.62 ± 0.27 (-0.007)
Max. horizontal distance (m)	0.16 ± 0.01 (-0.015)	0.23 ± 0.01 (0.041)	0.25 ± 0.01 (0.007)

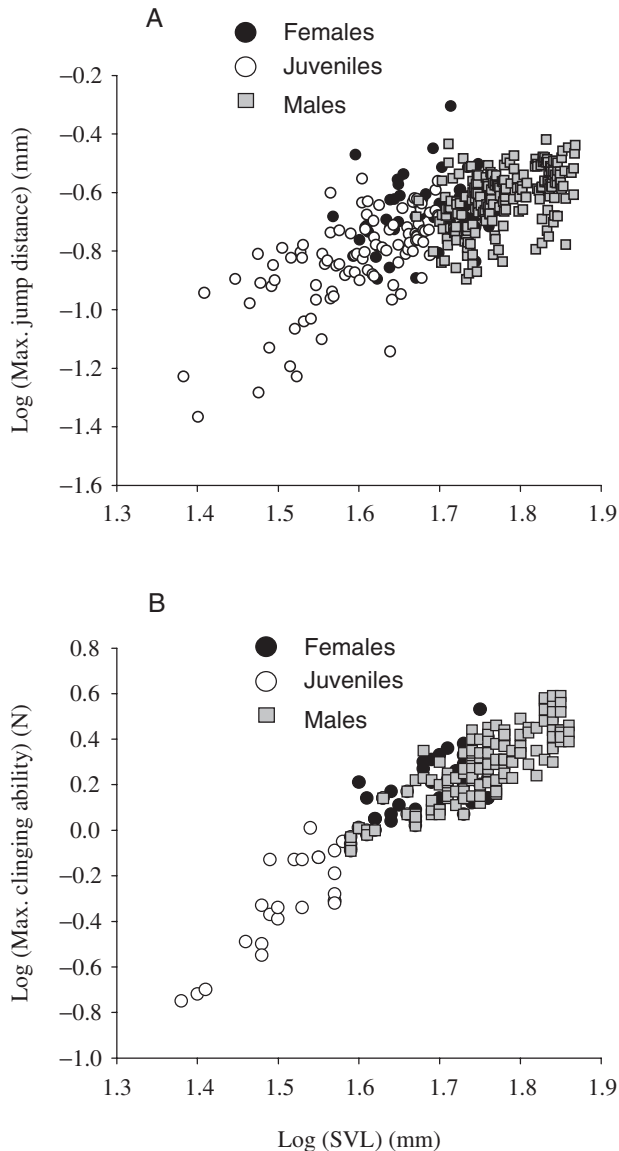


Figure 2. Scatterplots of log-transformed SVL (x -axis) vs. (A) log-transformed maximum jump distance, and (B) log-transformed clinging ability for all 403 green anoles. Each point is an individual. Note the different symbols denoting the different age/sex classes.

among the age/sex classes (Table 7). Females always had higher mean residual values for each variable, followed by males and then juveniles. Similarly, residual clinging ability differed significantly, with values for females higher than those for juveniles or males (one-way ANOVA, $F_{2,213} = 6.54$, $P < 0.01$; Table 6).

CANONICAL CORRELATION ANALYSIS

Only one of the three CCAs had a statistically significant canonical variate (morphology-performance, CV

1, Table 8); the others (morphology-habitat use and habitat use-performance) did not. Inspection of the loadings (Table 9) showed that hindlimb dimensions (femur and tibia length) both loaded highly for CV 1, as did maximum acceleration. In other words, across all age/sex classes, individuals with relatively longer hindlimbs tend to have relatively higher values of maximum jump acceleration.

DISCUSSION

Our data reveal several key findings. (1) Male, female and juvenile *A. carolinensis* differ significantly in size-adjusted morphology, habitat use, and jumping and clinging capacity. Specifically, females and males tended to use habitats with perches that were further apart (higher values of D_{np}) compared to juveniles. Therefore their microhabitat was slightly more 'open'. Males also had significantly longer hindlimb metatarsal elements (distal limb element) compared to females and juveniles, while females were more stocky compared to males and juveniles. Females were both better jumpers and clingers than males and juveniles. However, contrary to our original hypothesis, juveniles were always the worst performers (relative to size) compared to males (always second best) and females (always the best) for both jumping and clinging ability. (2) Our multivariate analyses show a significant positive correlation between hindlimb dimensions (femur, tibia) and maximum jump acceleration for all individuals. However, we found no significant correlations between size-adjusted morphology and habitat use, and between habitat use and size-adjusted jump capacity.

INTRASPECIFIC DIFFERENCES IN HABITAT USE AND PERFORMANCE

Previous studies on a wide variety of anole species have documented ecological niche segregation with regard to such aspects as prey type and habitat use (e.g. Schoener, 1968; Losos, 1994; Roughgarden, 1995; Herrel *et al.*, 2005). An implicit assumption of many of these studies is that these ecological differences have arisen to minimize intraspecific competition (Schoener, 1968).

Caribbean *Anolis* lizards have been studied intensively from this perspective, and previous studies have established that within several species, age and sex classes divide the habitat along both a perch height and perch diameter axis (Schoener, 1968; Schoener & Schoener, 1971a, b; Irschick *et al.*, 2000). Typically, the largest size class (males) perch on both broader and higher perches than females, which in turn perch on broader and higher perches than juveniles. Other research shows significant differentiation

Table 7. Results from either univariate ANOVAs (for the habitat PCA) or multivariate analyses of variance (MANOVA) for the morphological and performance data comparing three sex/age classes. Only results from significant differences among principal components or variables are shown

	<i>F</i>	d.f.	<i>P</i>
HABITAT			
PC 1	13.54	2371	< 0.001
Overall test (MORPHOLOGY)	6.06	6740	< 0.001
PC 1	7.54	2372	< 0.01
PC 2	9.92	2372	< 0.005
Overall test (JUMP PERFORMANCE)	3.18	6738	< 0.01
Residual max. distance	7.25	2371	< 0.01
Residual max. velocity	8.31	2371	< 0.005
Residual max. acceleration	9.22	2371	< 0.005

Table 8. Results from canonical correlation (CC) analyses between (1) morphology and habitat use*; (2) morphology and performance† and (3) performance and habitat use*

	CC	Chi-square	d.f.	<i>P</i>
(1) CV 1	0.254	40.28	45	< 0.50
(2) CV 1	0.267	45.92	27	< 0.01
(3) CV 1	0.150	14.49	15	> 0.40

*Tests were non-significant overall. Hence, values are only shown for the first CV.

†Values for only the first CV were shown because this was the only significant CC.

Table 9. Loadings for CCA relating morphology to jumping performance among individuals of all three classes. Substantial loadings for CV 1 are noted in bold

Variable	CV 1*	CV 2	CV 3
Mass	0.159	0.565	-0.237
Femur length	0.776	0.059	0.072
Tibia length	0.527	-0.019	-0.200
Metatarsal length	0.189	-0.453	0.210
Hind-toe	-0.113	-0.039	-0.339
Humerus	0.465	-0.510	-0.534
Radius	-0.031	0.157	0.014
Metatarsal	-0.304	0.448	-0.396
Fore-toe	0.065	-0.070	-0.384
Max. distance	0.093	0.835	-0.660
Max. velocity	0.068	0.745	-0.392
Max. acceleration	0.490	0.920	-0.251

*only CV that was statistically significant.

in diet among age/sex classes, typically on a functional basis, relating to prey size or hardness (Schoener, 1968; Herrel *et al.*, 2005). This suggests that age and sex classes occupy largely different niches to reduce competition.

Indeed, the environmental context within large Caribbean islands (e.g. Puerto Rico) seems ripe for intense intraspecific competition because of the relatively low diversity and abundance of insect prey, and the high density of often multiple sympatric species (Losos,

1994; Roughgarden, 1995). Our statistical analyses show that the primary difference among age/sex classes in a North American mainland population lies in the distance to nearest perches (D_{np}), which is significantly shorter for juveniles compared to males and females. Inspection of Table 1 shows that, on average, juveniles also tend to use narrower perches (mean = 2.5 cm) compared to females (mean = 5.4 cm) and males (mean = 4.0 cm) (see Jenssen & Nunez, 1998). By contrast, mean values of preferred perch height are very similar among the classes (Table 1). Thus, our data reveal limited niche segregation along a perch diameter but not height axis.

Why age/sex classes appear to segregate along a perch height axis in the Caribbean, but not in the North American mainland, is unclear. One possibility is that the vegetation at Good Hope Field is too short and simple, although it frequently exceeded 3 m, and appeared qualitatively similar to that of many Caribbean habitats (Irschick, pers. observ.). We did observe that juveniles often perched on the dense, terminal ends of branches on bushes and trees, which is consistent with their low D_{np} values, while adult males and females tended to prefer interior perches, such as tree trunks (Irschick, pers. observ.). Thus, juveniles may be segregating the habitat in part by occupying the more peripheral areas, which is not reflected in measures of perch height and diameter. The most obvious reason for this habitat choice is to avoid large males, which may consume or injure them (Herrel *et al.*, 2005). Another factor might be the availability of insect prey, which might be higher on peripheral branches, and would thus form an attractive microhabitat for juveniles that need to consume large amounts in order to grow rapidly. Studies that examine prey availability in different parts of anole habitats are required to help provide information on this issue.

VARIATION IN PERFORMANCE CAPACITY AMONG AGE/SEX CLASSES

Many researchers have documented interspecific variation in various aspects of performance capacity, with the usual interpretation being that such differences are adaptive (e.g. for occupying different habitats; see reviews by Pough, 1989; Garland & Losos, 1994; Irschick & Garland, 2001). Our multivariate analysis showed relatively weak ecomorphological relationships overall, with the only significant result being a positive relationship between the length of the hindlimb and maximum jump acceleration. This finding is consistent with interspecific studies showing a positive relationship between relative hindlimb dimensions and jump distance (Losos, 1990) and velocity and acceleration (Toro *et al.*, 2003, 2004).

Nevertheless, we did not find strong relationships among habitat use and morphology, suggesting that those documented for Caribbean anoles (Losos, 1990) are not apparent among individuals within a single North American mainland anole community. The fact that *A. carolinensis* occurs without any other sympatric species, in contrast to the situation in the Caribbean, might suggest that ecomorphological relationships may be more 'relaxed' in mainland North America.

However, we did document significant differentiation in relative performance capacities among age/sex groups. Such differences may be expected in reptiles due to the strong selective pressures that juveniles are likely to encounter (Carrier, 1996; Herrel *et al.*, 2005). Several authors have suggested that juveniles should 'compensate' for their poor absolute performance capacities by performing well relative to their size. Evidence for this view is equivocal. Irschick (2000) found that juvenile Jamaican *A. lineatopus* lizards tended to sprint more quickly (relative to size) compared to males and females when capturing prey in nature, and also when escaping a threat. A more recent analysis (Herrel *et al.*, 2005) examining bite forces and diet in the same species found concordant evidence that juveniles are good biters for their size, suggesting that they have compensated for having relatively weak absolute bite forces.

Our data here show a markedly different trend from these two studies. Females were always the best performers for all four size-adjusted performance variables (max. jump distance, velocity, acceleration, and clinging ability), followed by males and then juveniles. In short, contrary to the hypothesis of compensation, juveniles are worse jumpers and clingers in both absolute and relative terms.

Why females should perform better is unclear. Previous studies have shown that females in some lizard species, particularly when gravid, will exhibit behavioural shifts in escape behaviour (Bauwens & Thoen, 1981), but we are aware of no studies showing that female reptiles are better performers for their size compared to males or juveniles. One possible explanation for their enhanced clinging ability is that because they must climb when carrying eggs internally, they may have evolved this in order to provide an extra margin of safety.

It is also noteworthy that the age/sex classes did not differ significantly in size-adjusted toepad area, indicating that increases in clinging performance are not attributable to relatively larger areas, as has been shown for different species of pad-bearing lizards (Irschick *et al.*, 1996; Elstrott & Irschick, 2004). Indeed, relative toepad area and clinging ability were not significantly related among all individuals in this study ($r = 0.08$, $P > 0.25$), indicating that the same

mechanisms that increase clinging ability among anole species are not occurring within a single species. Further studies investigating the masses of eggs and relationships between survivorship and clinging in different age/sex classes would thus be useful. As a precautionary note, one must consider the possibility that performance differences may not always be of great importance. For example, most pad-bearing lizards possess far more clinging capacity than they actually need for everyday activities (Irschick *et al.*, 1996; Autumn *et al.*, 2000, 2002; Autumn & Peattie, 2002; Irschick *et al.*, 2003; Elstrott & Irschick, 2004), suggesting that females may not necessarily be at a great advantage.

Similarly, why females should be relatively better jumpers is unclear. Anole species jump regularly in nature, both during escape (Losos & Irschick, 1996), and during undisturbed locomotion (Irschick & Losos, 1998). However, an open issue is whether they use their maximal jumping capacities in nature; a variety of anole species readily sprint close to their maximum speeds when escaping from a threat (90% max. speed on average), or when capturing prey (70% max. speed on average; Irschick & Losos, 1998). Previous studies have shown that animal species with relatively long hindlimbs tend to be relatively good jumpers (Losos, 1990; Toro *et al.*, 2003), but our morphological analyses suggest that females do not have significantly longer hindlimbs compared to males and juveniles. Clearly, the best way to resolve whether natural selection may favour females with high performance capacities would be to conduct long-term mark-recapture studies on all age and sex classes of known jumping capacity and clinging ability.

In conclusion, we have documented significant differentiation in size-adjusted morphology, habitat use and size-adjusted performance capacity (jumping and clinging) among juveniles, females and males within the common green anole, *A. carolinensis*. In general, we found relatively weak multivariate relationships among the three aspects (morphology, habitat use and performance) across all individuals, although we did detect significant differences in both jumping and clinging ability among age/sex classes, suggesting some adaptive differentiation. Our hypothesis that juveniles should be better performers (relative to size) compared to adult females and males was disproven.

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