

# Determinants of sexual differences in escape behavior in lizards of the genus *Anolis*: a comparative approach

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**Synopsis** Males and females are known to differ in a whole suite of characteristics, such as morphology, physiology, ecology, and behavior. Intersexual differences are generally believed to arise because of differences in selective pressures on either sex. In this study, we investigated whether intersexual differences in escape behavior exist in lizards of the genus *Anolis*, and whether these could be explained by intersexual differences in body size and/or microhabitat use. To do so, we compared the behavioral response to an approaching human predator in the field in males and females of 12 *Anolis* species. We found that ecomorphs and sexes differ greatly with respect to escape behavior. Twig anoles have the shortest approach distance (i.e., distance between the observer and the lizard when it starts fleeing) and final distance (i.e., distance between the observer and the lizard when it stops moving), compared with the other ecomorphs. The distance fled, on the contrary, is greatest in twig anoles. Also, females flee less soon and run over shorter distances than do males. Since twig anoles are considered the most cryptic anoles, and females may be less conspicuous than males, these results corroborate the idea that well camouflaged animals allow predators to come closer. The interspecific variation in sexual dimorphism in escape behavior, however, cannot be explained by the interspecific variation in sexual size dimorphism or sexual dimorphism in microhabitat use. Thus, escape behavior appears determined by different factors in males and females.

## Introduction

Evolutionary biologists have long been fascinated by intersexual differences (Darwin 1871; Bajema 1984). Traditionally, sexual dimorphism has been interpreted as the result of differential selection pressures on males and females. Probably the most prominent and most frequently documented intersexual difference is that with regard to body size. Sexual size dimorphism has been shown to exist both in the plant and animal kingdoms, where it occurs across all known taxa (reviewed by Fairbairn 1997). Apart from intersexual differences in size, however, males and females may differ in a whole suite of characteristics. For instance, differences in shape (Butler and Losos 2002; Losos et al. 2003; Vincent 2006), physiology (Cullum 1998; Zuk and Stoehr 2002; Garcia-Falgueras et al. 2006; Markman et al. 2006), ecology (Butler and Losos 2002; Vincent 2006), performance (Cullum 1998; Herrel et al. 1999, 2001, 2006; Lailvaux et al. 2003), and behavior (e.g., Van Dijck 2003; Page et al. 2005; Lewis et al. 2006) have been demonstrated. As is the case with sexual size dimorphism, the existence of sexual dimorphism in the above-mentioned traits is traditionally explained by sexual selection, intersexual

resource partitioning, and/or different reproductive roles (Andersson 1994; Fairbairn 1997; Losos et al. 2003).

In this study, we focused on intersexual differences in escape behavior in lizards of the genus *Anolis*. Escape behavior is expected to be under strong natural selection as predation is probably one of the most pervasive selective agents for most organisms. Although a great diversity exists in predator avoidance strategies, most organisms try to move away at least at some point during a predator–prey encounter. The point at which they actually do so, depends on the balance between the costs of fleeing and those of remaining still. Since fleeing has costs in terms of energy and time taken away from other activities (e.g., foraging, defending territories), they should be traded off against the risk of capture. Only when predators are a serious threat, should the potential prey flee (Ydenberg and Dill 1986; Kramer and Bonenfant 1997). Both theoretical models and empirical data have shown that escape behavior depends on various environmental factors such as distance to a refuge (Bulova 1994; Kramer and Bonenfant 1997; Schulte et al.

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2004), habitat openness (Snell et al. 1988; Martín and López 1995a, 2000; Cuadrado et al. 2001; Schulte et al. 2004), and temperature (Bulova 1994; Smith 1997). Also predator traits such as the type of predator (Smith 1997; Hopper 2001), its abundance (Blazquez et al. 1997; Irschick et al. 2005), the direction of its approach (Cooper 1997a, 1997b; Vitt et al. 2002) and whether approaches are repeated (Cooper 1997a, 1997b; Regalado 1998; Díaz-Uriarte 1999; Martín and López 1999; Martín et al. 2000) are known to influence escape decisions. Additionally, escape strategies may be influenced by fixed characteristics inherently associated with the potential prey individual, such as its gender (Bauwens and Thoen 1981; Snell et al. 1988; Bulova 1994; Blazquez et al. 1997; Rodewald and Foster 1998; Shine et al. 2000; Lailvaux et al. 2003), age (Martín and López 1995b; Smith 1997; Cuadrado et al. 2001; Whiting et al. 2003), experience (Marcellini and Jenssen 1991; Regalado 1998), and social status (Díaz-Uriarte 1999).

We quantified the variation in escape behavior in male and female anoles and linked it to the variation in microhabitat use and body size. In doing so, we combined the effects of several of the above-mentioned factors known to influence escape decisions, i.e., habitat openness, body size, and sex. Moreover, in contrast to the majority of earlier studies on tactics of escape, we took an explicit comparative approach by contrasting escape strategies at the interspecific level. In doing so, we aimed at elucidating the evolutionary correlates of intersexual differences in escape behavior in anoles. We used anoles as our study system as they have evolved at least four times independently into a series of ecologically, behaviorally, and morphologically distinct forms, called ecomorphs (e.g., Williams 1983; Losos et al. 1998). Moreover, the degree of sexual dimorphism in size and shape varies among ecomorphs (Butler et al. 2000; Butler and Losos 2002; Losos et al. 2003) and within ecomorphs sexes differ with respect to microhabitat use (Butler and Losos 2002). Also, previous data suggest ecomorphs and sexes may differ in predator avoidance strategies (Heatwole 1968; Regalado 1998; Schneider et al. 2000; Cooper 2006).

In this study, we addressed two issues. First, we documented the variation in escape behavior among *Anolis* ecomorphs and between the sexes. Although this first part is purely descriptive, to address the subsequent question it is important to show that large variation in escape strategies does exist among ecomorphs and between the sexes. Second, we determined whether intersexual differences in

body size and use of microhabitat can explain the intersexual differences in escape behavior. We did so by testing whether the evolution of sexual dimorphism in escape behavior among anoles is correlated with the evolution of sexual dimorphism in habitat use and/or body size. In addition, we tested whether interspecific variation in escape behavior is explained by variation in the same ecological and morphological traits in males and females.

## Material and methods

### Species used

Between November 2001 and June 2002, we observed adult males and females of the following species of *Anolis*. On the mainland of the United States (Miami, Florida), we gathered observational data on *Anolis sagrei*, *A. distichus*, and *A. cristatellus*. *Anolis grahami*, *A. lineatopus* and *A. valencienni* were observed in Jamaica (Discovery Bay) and *A. cristatellus*, *A. evermanni*, *A. gundlachi*, *A. krugi*, *A. pulchellus*, and *A. stratulus* in Puerto Rico (El Verde). Although we refer to 12 species in the remainder of the text, strictly speaking our sample consisted of 11 different species and two populations of the same species (i.e., *A. cristatellus*).

For all species, adult males and females were captured at the same locations and their snout-vent lengths (SVL) measured to the nearest 0.01mm using digital calipers.

### Field observations

Microhabitat use and escape behavior in the field were quantified in the following way. We walked through each site slowly and haphazardly until a lizard was sighted. The observer positioned himself at a distance greater than 8 m from the lizard and started approaching it directly (i.e., in a straight line) walking at a constant speed ( $\pm 2 \text{ m s}^{-1}$ ). As soon as the lizard fled, the observer stopped moving towards it. If the initial perch was situated above our head, we attached a clipboard to the end of a 2 m pole and approached the lizard holding this construction up above our heads at the level of the lizard. Subsequently the following measurements were taken with a tape measure (accuracy of 0.01 m): perch height, perch diameter, approach distance, flight distance, and final distance. Both perch height and perch diameter were measured at the spot where the lizard was observed initially (cf. Losos 1990). Approach distance is defined as the distance between the lizard and the observer at the moment the lizard starts fleeing, flight distance as the distance between the

lizard's initial perch to the spot where it stopped moving, and final distance as the distance between the observer and the spot where the lizard stopped moving, measured in a straight line (cf. Bauwens and Thoen 1981; Bulova 1994). We note that approach distance as defined here has been termed flight (initiation) distance by others (e.g., Ydenberg and Dill 1986). If lizards ran into a hiding place (e.g., into a crevice, under leaf litter), flight distance was measured as the distance between the lizard's initial perch and the entrance of the hiding place. We also recorded the type of substrate on which the lizard was sitting when sighted (perch substrate) and the type of substrate to which it escaped (escape substrate). Six substrate types were discerned in both cases: (1) trunk, (2) branch, (3) twig, (4) ground/leaf litter, (5) grass/herbs, and (6) stone wall. We minimized the chance of observing the same individual twice by walking different sections of the field sites as much as possible.

### Statistical analyses

Variation among ecomorphs and between sexes

We calculated mean approach distance, flight distance and final distance for each species separately by gender and logarithmically ( $\log_{10}$ ) transformed the data prior to subsequent statistical analyses.

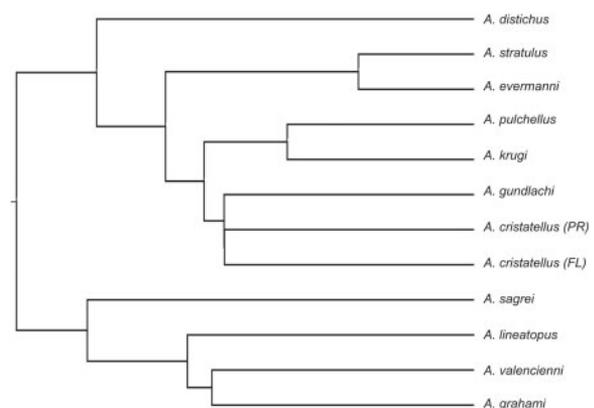
To document whether ecomorphs and sexes differ with respect to escape behavior, we performed a two-way Multivariate Analysis of Variance (MANOVA) with ecomorph and sex entered as factors and approach, flight and final distance as dependents. Subsequently, a *post hoc* comparison (Tukey) was done to test for differences between pairs of ecomorphs.

To test for differences in substrate use among ecomorphs and sexes before and after being disturbed, we performed a hierarchical loglinear analysis in which ecomorph, sex, perch substrate and escape substrate were entered as factors. By entering both perch substrate and escape substrate we tested whether the substrate on which a lizard was initially sighted affects its use of substrate when escaping. Preliminary analyses, however, showed that in most cases, individual lizards did not change substrate. To test whether perch substrate affects escape substrate when individuals do change substrates, we entered "no change" in substrate use as a separate type of escape substrate. Thus, escape substrate was coded from one to seven in the following way: escape substrate equals (1) perch substrate, (2) trunk, (3) branch, (4) twig, (5) ground/leaf litter, (6) grass/herbs, and (7) stone wall.

### Determinants of intersexual differences

Apart from mean approach distance, flight distance and final distance for each species separately by sex, we calculated the mean SVL, perch height and perch diameter. In addition, we calculated sexual dimorphism in SVL, perch height and perch diameter and the three escape behavior variables as the ratio of the value of each trait in males to that in females (cf. Butler et al. 2000; Losos et al. 2003). Both the "raw" values and the estimates of sexual dimorphism were subsequently logarithmically ( $\log_{10}$ ) transformed.

Since species share parts of their evolutionary history, they cannot be regarded as independent data points in statistical analyses (Felsenstein 1985, 1988; Harvey and Pagel 1991). However, several methods and computer programs have been developed over the years in which phylogenetic relationships among different species can be taken into account in statistical analyses (Felsenstein 1985, 1988; Harvey and Pagel 1991; Losos and Miles 1994). In this study, we used both Monte Carlo simulations (Garland et al. 1993) and the independent contrast approach (Felsenstein 1985, 1988). Both approaches require information on the topology and branch lengths of the phylogenetic tree. The phylogeny of the 11 *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](http://biosgi.wustl.edu/~lososlab/anolis_mbg_2005)) and upon request from



**Fig. 1** Phylogenetic relationships among the 11 *Anolis* species and two populations of *A. cristatellus* used in this study. The phylogenetic tree is based on mitochondrial DNA (Nicholson et al. 2005). In the analyses, the node connecting the two *A. cristatellus* populations was placed as deep as possible for the two populations to still be monophyletic (L. Harmon, personal communication, ). Branch lengths are to scale.

K. Nicholson. The node connecting the two *A. cristatellus* populations was placed as deep as possible for the two populations to still be monophyletic (L. Harmon, personal communication.). We checked whether branch lengths were adequate by correlating the absolute values of the standardized contrasts to their standard deviations (PDTREE program; Garland et al. 1999). If the correlation was significant (i.e., branch lengths not adequate), we transformed the branch lengths using a rho-transformation with  $\rho = 0.01$ .

We tested whether ecomorphs differ in degree of sexual dimorphism in approach distance, flight distance and final distance by conducting a phylogenetic ANOVA with ecomorph as a factor. First, 1000 Monte Carlo simulations of character evolution along the branches of the phylogenetic tree were carried out for each of the three variables separately (PDSIMUL; Garland et al. 1993). Then, one-way ANOVAs with ecomorph as factor were carried out on the 1000 simulated data sets, and a “phylogenetic” null distribution of *F*-values created for each trait (PDANOVA; Garland et al. 1993). If the *F*-values obtained from the “traditional” ANOVAs 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 sexual dimorphism in approach distance, flight distance and final distance, because previous studies have already documented differences in sexual dimorphism in size and habitat among ecomorphs (Butler et al. 2000; Butler and Losos 2002; Losos et al. 2003).

Standardized independent contrasts for all “raw” variables (i.e., SVL, perch height and diameter, approach distance, flight distance, and final distance) as well as for the estimates of sexual dimorphism were calculated using the PDTREE program (Garland et al. 1999). All subsequent regressions were forced through the origin (see Garland et al. 1999).

To test whether the interspecific variation in sexual dimorphism in escape behavior is explained by the variation in sexual dimorphism in SVL and/or microhabitat use, we performed regression analyses with the contrasts in sexual dimorphism in one of the escape behavior traits as the dependent variable and the contrasts in sexual dimorphism in SVL, perch height, and perch diameter as independent variables (backward method; regressions forced through the origin, Garland et al. 1999).

Subsequently we performed similar regression analyses for each sex to test whether similar relations

exist among escape behavior, body size, and microhabitat use in males and females. In these cases, we entered the contrasts in one of the escape-behavior traits as the dependent variable and the contrasts in SVL, perch height, and perch diameter as independent variables into a multiple regression model (backward method; regressions forced through the origin, Garland et al. 1999). Also in the regression models with flight distance and final distance as dependent variables, we included the contrasts in approach distance as another independent variable, and the contrasts in approach and flight distance as independent variables, respectively.

## Results

Averages and standard errors of SVL, perch height, perch diameter, approach distance, flight distance, final distance, and sample sizes for each species and sex are given in Table 1.

### Variation among ecomorphs and between sexes

The two-way MANOVA on approach, flight distance and final distance shows a significant ecomorph by sex interaction effect ( $F_{12,42} = 1.99$ ,  $P = 0.05$ ), as well as a significant ecomorph ( $F_{12,42} = 5.80$ ,  $P < 0.0001$ ) and sex effect ( $F_{3,12} = 27.10$ ,  $P < 0.0001$ ). When considering the three variables separately, the interaction effect is only significant for approach distance, whereas both approach distance and flight distance are significantly different between sexes, and all three variables differ among ecomorphs (Table 2). Approach distance in twig anoles differs significantly from approach distance in all other ecomorphs (Tukey *post hoc* comparison: all  $P < 0.001$ ). It is shortest in twig anoles and greatest in trunk-ground and grass-bush anoles. Approach distance does not differ significantly when comparing all other ecomorph groups among one another (Tukey *post hoc* comparison: all  $P > 0.17$ ). Females allow closer approaches than do males, except in trunk-crown anoles (Fig. 2A). Similarly, flight distance in twig anoles differs significantly from flight distance in all other ecomorphs (Tukey *post hoc* comparison: all  $P < 0.046$ ). It is greatest in twig anoles and similar in all other ecomorphs (Fig. 2B). Again, flight distance does not differ when comparing all other ecomorphs among one another (Tukey *post hoc* comparison: all  $P > 0.13$ ). Final distance only differs significantly between twig and trunk-ground anoles and between twig and grass-bush anoles (Tukey *post hoc* comparison: both  $P < 0.002$ ). Similarly to approach distance, final distance is shortest in twig anoles and greatest in trunk-ground and grass-bush anoles. All other

**Table 1** Averages  $\pm$  standard errors of SVL, perch height, perch diameter, approach distance, flight distance, and final distance, for each species and sex. Sample sizes for measurements of SVL ( $N_{\text{SVL}}$ ) and field observations ( $N_{\text{field}}$ ) are given. Ecomorph letter codes are: GB = grass-bush; TG = trunk-ground; TC = trunk-crown; TR = trunk; TW = twig

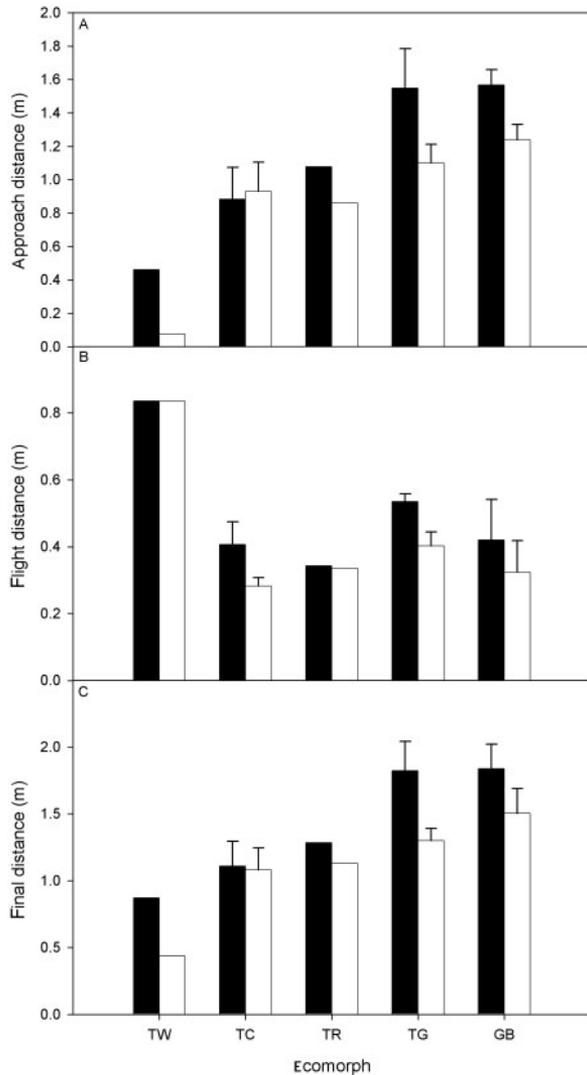
Species	Ecomorph	Sex	$N_{\text{SVL}}$	SVL (mm)	$N_{\text{field}}$	Perch height (m)	Perch diameter (m)	Approach distance (m)	Flight distance (m)	Final distance (m)
<i>A. krugi</i>	GB	M	39	39.64 $\pm$ 1.06	32	0.63 $\pm$ 0.12	1.08 $\pm$ 0.30	1.66 $\pm$ 0.14	0.54 $\pm$ 0.07	2.02 $\pm$ 0.14
		F	14	31.97 $\pm$ 1.41	6	0.30 $\pm$ 0.12	1.33 $\pm$ 0.84	1.33 $\pm$ 0.27	0.42 $\pm$ 0.07	1.69 $\pm$ 0.33
<i>A. pulchellus</i>	GB	M	39	42.05 $\pm$ 0.65	23	0.28 $\pm$ 0.06	0.70 $\pm$ 0.32	1.47 $\pm$ 0.12	0.30 $\pm$ 0.03	1.65 $\pm$ 0.09
		F	7	40.09 $\pm$ 1.59	6	0.33 $\pm$ 0.08	0.02 $\pm$ 0.01	1.15 $\pm$ 0.11	0.23 $\pm$ 0.02	1.32 $\pm$ 0.11
<i>A. gundlachi</i>	TG	M	52	55.26 $\pm$ 1.41	35	1.29 $\pm$ 0.09	0.56 $\pm$ 0.12	1.51 $\pm$ 0.14	0.57 $\pm$ 0.07	1.77 $\pm$ 0.15
		F	19	46.02 $\pm$ 0.56	21	0.98 $\pm$ 0.13	0.79 $\pm$ 0.24	1.53 $\pm$ 0.15	0.35 $\pm$ 0.06	1.63 $\pm$ 0.15
<i>A. cristatellus</i> (PR)	TG	M	49	64.50 $\pm$ 1.23	17	1.18 $\pm$ 0.11	1.13 $\pm$ 0.40	1.32 $\pm$ 0.27	0.46 $\pm$ 0.10	1.63 $\pm$ 0.26
		F	42	46.64 $\pm$ 0.53	16	0.71 $\pm$ 0.09	0.73 $\pm$ 0.33	1.07 $\pm$ 0.17	0.33 $\pm$ 0.05	1.27 $\pm$ 0.18
<i>A. cristatellus</i> (FL)	TG	M	28	61.21 $\pm$ 1.77	28	0.91 $\pm$ 0.15	1.44 $\pm$ 0.40	2.17 $\pm$ 0.47	0.53 $\pm$ 0.06	2.28 $\pm$ 0.47
		F	12	48.83 $\pm$ 1.41	12	0.84 $\pm$ 0.21	1.90 $\pm$ 0.54	1.02 $\pm$ 0.17	0.49 $\pm$ 0.10	1.21 $\pm$ 0.16
<i>A. evermanni</i>	TC	M	60	55.57 $\pm$ 0.87	23	1.17 $\pm$ 0.12	1.10 $\pm$ 0.29	1.25 $\pm$ 0.19	0.44 $\pm$ 0.08	1.48 $\pm$ 0.20
		F	44	46.36 $\pm$ 0.61	10	1.31 $\pm$ 0.23	0.23 $\pm$ 0.05	1.11 $\pm$ 0.19	0.30 $\pm$ 0.08	1.25 $\pm$ 0.18
<i>A. stratulus</i>	TC	M	38	44.95 $\pm$ 0.33	25	1.47 $\pm$ 0.14	0.52 $\pm$ 0.16	0.78 $\pm$ 0.13	0.27 $\pm$ 0.03	0.92 $\pm$ 0.14
		F	28	37.78 $\pm$ 0.47	12	1.40 $\pm$ 0.20	0.86 $\pm$ 0.34	1.10 $\pm$ 0.30	0.24 $\pm$ 0.04	1.24 $\pm$ 0.31
<i>A. distichus</i>	TR	M	17	47.54 $\pm$ 0.83	25	0.77 $\pm$ 0.09	1.08 $\pm$ 0.13	1.08 $\pm$ 0.16	0.34 $\pm$ 0.02	1.29 $\pm$ 0.16
		F	13	43.57 $\pm$ 0.46	17	0.83 $\pm$ 0.13	0.80 $\pm$ 0.09	0.86 $\pm$ 0.12	0.34 $\pm$ 0.03	1.13 $\pm$ 0.12
<i>A. grahami</i>	TC	M	23	59.63 $\pm$ 0.92	23	1.73 $\pm$ 0.19	0.81 $\pm$ 0.22	0.62 $\pm$ 0.12	0.32 $\pm$ 0.04	0.93 $\pm$ 0.11
		F	17	45.21 $\pm$ 0.81	20	1.35 $\pm$ 0.17	0.38 $\pm$ 0.07	0.58 $\pm$ 0.14	0.32 $\pm$ 0.04	0.75 $\pm$ 0.13
<i>A. lineatopus</i>	TG	M	57	51.63 $\pm$ 0.78	14	0.71 $\pm$ 0.13	0.61 $\pm$ 0.28	0.82 $\pm$ 0.19	0.52 $\pm$ 0.11	1.14 $\pm$ 0.21
		F	44	44.01 $\pm$ 0.34	22	0.80 $\pm$ 0.11	0.49 $\pm$ 0.18	0.89 $\pm$ 0.11	0.33 $\pm$ 0.03	1.09 $\pm$ 0.12
<i>A. valencienni</i>	TW	M	25	65.47 $\pm$ 1.65	5	1.43 $\pm$ 0.31	0.43 $\pm$ 0.15	0.46 $\pm$ 0.15	0.84 $\pm$ 0.34	0.87 $\pm$ 0.21
		F	22	59.38 $\pm$ 1.39	2	0.66 $\pm$ 0.51	0.06 $\pm$ 0.01	0.08 $\pm$ 0.03	0.84 $\pm$ 0.32	0.44 $\pm$ 0.01
<i>A. sagrei</i>	TG	M	25	56.20 $\pm$ 1.16	22	0.36 $\pm$ 0.08	2.25 $\pm$ 0.39	1.91 $\pm$ 0.38	0.60 $\pm$ 0.09	2.30 $\pm$ 0.41
		F	10	43.85 $\pm$ 0.95	17	0.36 $\pm$ 0.11	2.11 $\pm$ 0.45	1.01 $\pm$ 0.14	0.52 $\pm$ 0.06	1.30 $\pm$ 0.12

**Table 2** Results from the two-way MANOVA with ecomorph and sex as factors, and approach, flight, and final distance as dependent variables. Shown are the results for each dependent separately. Significant *P*-values are shown in bold.

Factor	Dependent	df	<i>F</i>	<i>P</i>
Ecomorph	Approach distance	4, 14	18.25	<b>&lt;0.0001</b>
	Flight distance	4, 14	6.51	<b>0.004</b>
	Final distance	4, 14	7.96	<b>0.001</b>
Sex	Approach distance	1, 14	11.47	<b>0.004</b>
	Flight distance	1, 14	2.33	0.149
	Final distance	1, 14	5.47	<b>0.035</b>
Ecomorph $\times$ sex	Approach distance	4, 14	3.64	<b>0.031</b>
	Flight distance	4, 14	0.31	0.864
	Final distance	4, 14	0.85	0.518

pairwise comparisons are non-significant (Tukey *post hoc* comparison: all  $P > 0.08$ ). The total distance covered by females is shorter than in males for all ecomorphs (Fig. 2C).

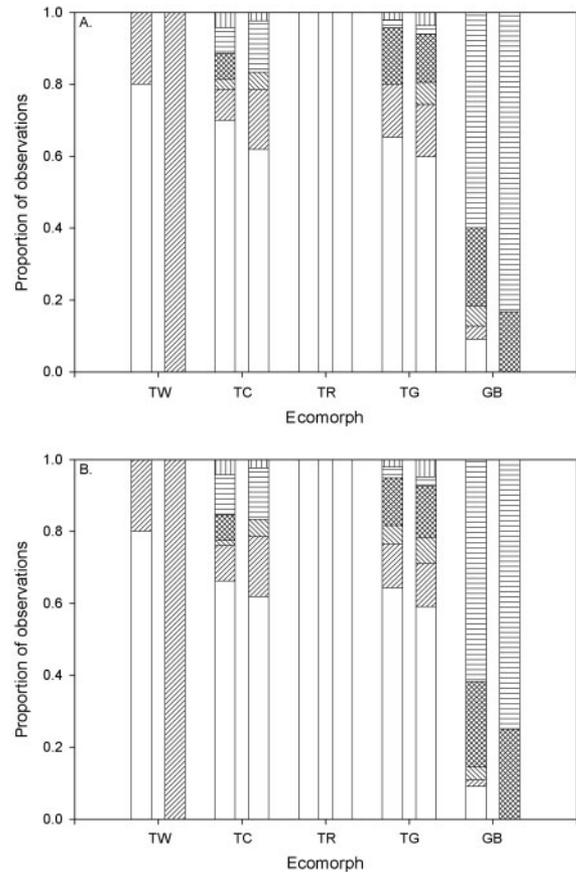
The hierarchical loglinear analysis with ecomorph, sex, perch substrate, and escape substrate as factors results in a “best” model ( $\chi^2 = 62.01$ ,  $df = 325$ ,  $P = 1.00$ ) in which the interactions between ecomorph and escape substrate ( $\chi^2 = 36.71$ ,  $df = 24$ ,  $P = 0.05$ ), between ecomorph and perch substrate ( $\chi^2 = 211.81$ ,  $df = 20$ ,  $P < 0.0001$ ), between perch and escape substrate ( $\chi^2 = 79.68$ ,  $df = 30$ ,  $P < 0.0001$ ), and between ecomorph and sex ( $\chi^2 = 18.30$ ,  $df = 4$ ,  $P = 0.001$ ) are included. Except for the number of observations per sex per ecomorph, none of the other variables show significant intersexual differences. Ecomorphs, on the other hand, differ with respect to both perch and escape substrate. Whereas trunk anoles are solely observed on tree trunks in both cases, twig anoles are also seen on branches, and grass-bush anoles are mostly observed in the grass. Both trunk-ground and trunk-crown anoles seem to occupy a range of substrates (Fig. 3). Also, perch substrate greatly affects escape substrate.



**Fig. 2** Bar plot of average and standard error (vertical bars) in escape behavior for different ecomorphs and sexes. (A) Approach distance, (B) flight distance, (C) final distance. Color of bar refers to the sexes (black = males; white = females). Letter codes refer to the five ecomorphs (TW = twig; TC = trunk-crown; TR = trunk; TG = trunk-ground; GB = grass-bush).

Although in most cases lizards escape towards (or stay on) the same substrate as the one on which they were initially sighted, when they did change substrate, individuals on the stone wall, branches, and in the grass escaped towards the ground and/or tree trunks, whereas individuals seen on twigs or on the ground escaped primarily to grass.

The ecomorph-by-sex interaction suggests that the number of observations (in this case individuals) per sex differs among ecomorphs. This is indeed the case (Table 1). Since it is unlikely that this sampling artifact changes the results and/or the interpretation thereof, we will not explicitly discuss the effect of this particular interaction further.



**Fig. 3** Stacked bar plot representing the proportion of time the different ecomorphs and sexes were observed on each substrate type. (A) Perch substrate, (B) escape substrate. Letter codes refer to the five ecomorphs (TW = twig; TC = trunk-crown; TR = trunk; TG = trunk-ground; GB = grass-bush). Within ecomorphs, data for males are represented by the left bar, data for females by the right bar. Patterns refer to substrate types (open = trunk; hatched to left = branch; hatched to right = twig; crosshatched = ground; horizontal stripes = grass; vertical stripes = stone wall).

### Determinants of intersexual differences

Phylogenetic ANOVA's with ecomorph as a factor show a significant difference in degree of sexual dimorphism in approach distance ( $F_{\text{trad}} = 6.69$ ,  $F_{\text{phyl}} = 5.67$ ,  $p_{\text{phyl}} = 0.038$ ). Twig anoles are extremely dimorphic in approach distance, followed by trunk-ground anoles. Trunk and grass-bush anoles show similar levels of sexual dimorphism in approach distance. In trunk-crown anoles, sexual dimorphism in approach distance is  $<1$ , meaning that males let a predator come closer than do females (see also Fig. 2). The different ecomorphs do not differ with respect to degree of sexual dimorphism in either flight distance or final distance ( $F_{\text{trad}} = 1.44$  and  $1.45$ ,  $F_{\text{phyl}} = 5.25$  and  $5.48$ ,  $p_{\text{phyl}} = 0.442$  and  $0.427$ , respectively).

The multiple regression with the contrasts in sexual dimorphism in approach distance as a dependent variable and the contrasts in sexual dimorphism in SVL, perch height, and perch diameter as independent variables did not result in a significant model ( $r=0.64$ ,  $F_{3,8}=1.86$ ,  $P=0.21$ ). Thus, the variation in sexual dimorphism in body size or perch characteristics cannot explain a significant proportion of the variation in sexual dimorphism in approach distance. Similarly, the variation in sexual dimorphism in flight distance or in final distance cannot be explained by the variation in sexual dimorphism in SVL, perch height, or perch diameter ( $r=0.50$ ,  $F_{3,8}=0.90$ ,  $P=0.48$  and  $r=0.53$ ,  $F_{3,8}=1.05$ ,  $P=0.42$ ).

When analyzing the sexes separately, the multiple regression with the contrasts of approach distance as a dependent variable and the contrasts in SVL, perch height, and perch diameter as independent ones resulted in a significant model both for males ( $r=0.77$ ,  $F_{1,10}=14.16$ ,  $P=0.004$ ) and for females ( $r=-0.57$ ,  $F_{1,10}=4.90$ ,  $P=0.051$ ). Only the contrasts in perch diameter are retained in the model for males, whereas for females only the contrasts in SVL are retained.

The multiple regression with the contrasts of flight distance as a dependent variable and the contrasts in SVL, perch height, perch diameter, and approach distance as independent variables resulted in a significant model for females ( $r=0.95$ ,  $F_{4,7}=14.65$ ,  $P=0.002$ ) and a marginally non-significant one for males ( $r=0.55$ ,  $F_{1,10}=4.42$ ,  $P=0.06$ ). Whereas in males, the variation in contrasts in SVL tends to correlate positively with the variation in contrasts in flight distance, in females all variables are retained in the model. The contrasts in SVL and perch diameter are positively partially correlated to the contrasts in flight distance ( $r_{\text{part}}=0.76$ ,  $P=0.018$  and  $r_{\text{part}}=0.89$ ,  $P=0.001$  respectively), whereas the contrasts in perch height and approach distance are negatively partially correlated to the contrasts in flight distance ( $r_{\text{part}}=-0.81$ ,  $P=0.008$  and  $r_{\text{part}}=-0.82$ ,  $P=0.007$ ).

Lastly, the multiple regression with the contrasts of final distance as dependent variable and the contrasts of SVL, perch height, perch diameter, approach distance, and flight distance as independent variables resulted in a significant model both for males ( $r=0.99$ ,  $F_{3,8}=502.79$ ,  $P<0.0001$ ) and for females ( $r=0.96$ ,  $F_{2,9}=47.62$ ,  $P<0.0001$ ). In males, the contrasts in perch height are negatively correlated with the contrasts in final distance ( $r_{\text{part}}=-0.73$ ,  $P=0.016$ ), whereas the contrasts in approach distance and flight distance are positively correlated

to the contrasts in final distance ( $r_{\text{part}}=0.97$ ,  $P<0.0001$  and  $r_{\text{part}}=0.96$ ,  $P<0.0001$ , respectively). In females, the variation in the contrasts in approach distance and flight distance are the sole predictors of the variation in the contrasts in final distance ( $r_{\text{part}}=0.95$ ,  $P<0.0001$  and  $r_{\text{part}}=0.60$ ,  $P=0.051$ , respectively).

## Discussion

### Differences in escape behavior among ecomorphs and between the sexes

We realize our analyses for this first part do not take into account phylogenetic relatedness among the different species. However, it is impossible to execute a two-way phylogenetic (M)ANOVA. Thus the results of these analyses should be considered as descriptive only.

Escape behavior varies greatly among ecomorphs and between sexes. Twig anoles allow predators to come significantly closer before they start fleeing compared with the four other ecomorphs, which are all similar with regards to approach distance. As for flight distance, twig anoles flee over greater distances compared with the four other ecomorphs, that all flee over similar distances. The differences in final distance mirror those in approach distance. Variation in escape decisions among trunk-crown, trunk, trunk-ground, and grass-bush anoles have been documented in the literature (Heatwole 1968; Regalado 1998; Schneider et al. 2000; Cooper 2006). These ecomorph differences have been associated with differences in degree of conspicuousness, at least to human predators, between trunk-crown and trunk-ground anoles (Heatwole 1968), and differences in microhabitat structure, such as openness (Regalado 1998; Schneider et al. 2000; Cooper 2006). Similar reasonings have been used to explain variation in escape behavior in other lizard species (e.g., Snell et al. 1988; Martín and López 1995a, 2000; Cuadrado et al. 2001; Schulte et al. 2004). To our knowledge, no empirical data on escape behavior in twig anoles is available. Twig anoles are generally considered the most cryptic ecomorph (Hicks and Trivers 1983; Irschick and Losos 1996). Their extremely short approach distances, as compared with the other ecomorphs, thus corroborate the idea that well camouflaged animals allow predators to come closer (cf. Heatwole 1968). Twig anoles, on the other hand, have the longest flight distances. Thus, once twig anoles start running, they move over great distances, suggesting that they compensate for their short approach distance (cf. Bulova 1994).

Ecomorphs also differ with respect to substrate use, both prior and after disturbance by a human “predator.” Our results on substrate use are consistent with the traditional ecomorph concept (Rand 1964, 1967; Schoener 1968; Williams 1983; Losos 1990; Losos et al. 1998). Similar patterns are evident for escape substrate as it is primarily a consequence of perch substrate. Since there is no interaction effect between perch substrate, escape substrate, ecomorph and/or sex, the same is true for all ecomorphs and both sexes. In fact, in most cases lizards stay on their initial type of substrate. As has been suggested for other lizard species, anoles might choose to escape to substrates with which they are familiar (Vitt et al. 2002), or to their “preferred” substrates (Vanhooydonck and Van Damme 2003). Since performance is expected to be better in familiar or preferred microhabitats, escaping towards (or staying on) these specific locations may increase an animal’s chances of surviving a predatory attack.

Our data also show clear sexual differences in escape decisions. Apart from trunk-crown anoles, females have shorter approach distance and final distances than males. Thus, in most cases, female anoles allow a potential predator to come closer before they start fleeing and they do not flee as far from the predator. The distance over which the lizards actually ran (i.e., flight distance), however, does not differ between the sexes. Results from other studies comparing escape decisions in male and female lizards are not clear-cut. Whereas males have shorter approach distances than females in lava lizards (Snell et al. 1988), males flee sooner than do females in other lizard species (Heatwole 1968; Bauwens and Thoen 1981; Lailvaux et al. 2003; Cooper 2006), or may even adopt similar escape strategies (Bulova 1994; Blazquez et al. 1997; Whiting et al. 2003). Similarly, flight distance may (Bauwens and Thoen 1981) or may not (Snell et al. 1988; Lailvaux et al. 2003; Whiting et al. 2003) differ between the sexes. Snell et al. (1988) suggested that highly territorial male lava lizards flee less soon because they might risk losing their territory if they flee unnecessarily. Since we found the opposite pattern (i.e., males flee sooner than females) in *Anolis*, that, except for twig anoles, are presumed to be highly territorial (Schoener and Schoener 1980, 1982; Hicks and Trivers 1983), we do not believe territoriality can explain the intersexual difference in escape strategies we observed. As suggested by other researchers (cf. Heatwole 1968; Bauwens and Thoen 1981; Cooper 2006), their being less conspicuous, suffering from impaired locomotory

capacities, or using different perches are more likely explanations for the greater approach distances in females.

### Determinants of intersexual differences

The phylogenetic ANOVA’s on the three components of escape behavior are consistent with the results from the two-way MANOVA’s discussed earlier. Anole ecomorphs differ in degree of sexual dimorphism in approach distance. Whereas in four out of the five ecomorphs, males flee sooner than do females (dimorphism  $>1$ ), in trunk-crown anoles females flee sooner (see also above). Also, the difference between males and females in approach distance is extremely large in twig anoles. In this ecomorph, females wait extremely long before they start fleeing. The females’ highly cryptic behavior might be a possible explanation (see above). Degree of dimorphism in flight distance and final distance, on the other hand, is similar in all ecomorphs. Females flee over smaller distances in all cases (see above).

The results from the regression analyses show that the sexual dimorphism in escape behavior among *Anolis* lizards cannot be explained by the sexual dimorphism in size and/or microhabitat use. Similar analyses on the sexes separately learn that different (combinations of) morphological and ecological variables explain the variation in all three quantified components of escape behavior in males and females. Among male *Anolis* species, the evolution towards using broader perches has been paralleled by the evolution towards earlier fleeing (i.e., greater approach distances). Typically broader substrates, such as the ground, leaf litter, and large tree trunks, are also more open microhabitats. Since in open microhabitats animals are less concealed and more conspicuous to predators, they tend to flee sooner (Snell et al. 1988; Martín and López 1995a, 2000; Schulte et al. 2004). This does not seem to hold true for females, however. Among female anoles, the variation in body size seems to be the sole predictor (of the variables under study here) of the variation in approach distance. Here, an increase in body size resulted in a decrease in approach distance. Previous studies specifically addressing the effect of body size on escape behavior have shown the opposite pattern, namely bigger individuals flee sooner (Heatwole 1968; Martín and López 1995b; Cuadrado et al. 2001; Whiting et al. 2003). It has been suggested that being less conspicuous, not being able to run as fast as large individuals, or using an “imperfect” escape response drives smaller individuals to wait longer

before they actually start fleeing (Heatwole 1968; Marcellini and Jenssen 1991; Martín and López 1995b; Cuadrado et al. 2001; Whiting et al. 2003). All these studies, however, have compared juveniles with adults within one species. Clearly, different, as yet undefined, factors explain the interspecific pattern observed here.

By contrast, the variation in body size explains the variation in flight distance in males. In this case, the evolution towards larger animals has been paralleled by an evolution towards a greater flight distance. This result is consistent with results from comparisons between juvenile and adult lizards (Martín and López 1995b; Whiting et al. 2003). Possibly, because of their larger body size, and potentially greater running speeds, larger animals cover a greater distance in a given time than do small lizards. In females, on the other hand, the situation is more complex as the variation in flight distance is explained by the combination of a whole suite of traits. First, all else being equal, approach and flight distance are negatively correlated. This suggests that, as may be the case with twig anoles (see above), female anoles with small approach distances compensate by fleeing over greater distances (cf. Bulova 1994). Further, flight distance depends on microhabitat in such a way that flight distance increases when females occupy more open habitats (i.e., lower perch height and broader substrates). Open habitats typically do not offer effective hiding spots and thus animals may need to run over greater distances to reach a safe refuge (Martín and López 2000; Vanhooydonck and Van Damme 2003). Lastly, as is the case in males, an increase in body size is correlated with an increase in flight distance in females (see above).

Finally, also the relationship between final distance and body size and/or ecology differs between males and females. Whereas in female anoles, the interspecific variation in final distance is solely explained by the variation in approach distance and final distance, the interspecific variation among males is also explained by variation in microhabitat (i.e., perch height). Thus, the evolution towards perching higher has been paralleled by evolution toward escaping at shorter actual distances between lizard and predator (observer). Probably, a human, terrestrial, predator represents less of a threat to animals sitting high up in a tree. Escaping over a small distance may be enough to be out of reach in such a case (Cooper 2006). We also note that a clipboard on a pole was used as “predator” in some of the trials in which lizards were perched very high up in a tree. We do not believe the different

kinds of predator are responsible for our results as no correlation between final distance and perch height was apparent in females. However, using a different method from other studies may make our results not directly comparable.

Why does escape behavior appear to be determined by other morphological and ecological traits in male and female anoles? We suggest that female anoles may be generally more cryptic and better camouflaged than are males. This idea is corroborated by data on one species of *Anolis*. Heatwole (1968) showed that female *A. cristatellus* are less conspicuous, at least to human observers, than are males. If females do indeed rely more on crypsis than on running away to avoid predation, other ecological factors may determine their escape decisions. For instance, cryptic animals may decide when to start fleeing depending on the degree of background matching (cf. Cuadrado et al. 2001) and not on habitat openness *per se*. To test this idea, however, one needs data on how well camouflaged males and females of the different species are in their respective environments.

Surprisingly, we found that flight distance is related in a complex way to other traits in females but not in males. Since (even cryptic) animals are very conspicuous once they start moving, it may be beneficial to flee as far as possible and away from open habitats (cf. Martín and López 2000). However, flight distance may not be determined by habitat characteristics *per se* in males, as male anoles are highly territorial and potentially cannot risk losing their perch to another male. This probably does not apply to females and thus adjusting flight distance as a function of microhabitat use may increase their chances of survival.

## Conclusions

Escape behavior in anoles seems to differ among ecomorphs and between the sexes. The degree of sexual dimorphism in either component of escape behavior can be explained by the degree of sexual size dimorphism in body size or microhabitat use, since a different combination of factors seem to determine escape decisions in males than in female anoles. This study also shows that intersexual differences may be substantial, thus warranting not unconditional pooling of data for males and females. Also, it is clear that selective pressures on males and females are different and results for either sex do not necessarily apply to the other.

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