

Differential growth of naturally and sexually selected traits in an *Anolis* lizard

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Abstract

Sexual dimorphism may be indicative of differential natural and/or sexual selection pressures acting on males and females. Although similar degrees of adult sexual dimorphism may be observed among populations and species, underlying physiological, developmental and ecological processes driving growth during the juvenile stages may vary. Unraveling how and when differences arise during ontogeny is important to our understanding of the evolutionary patterns observed among adults. In addition, growth patterns may differ among traits within a single individual. *Anolis* lizards vary greatly in the degree of adult sexual size and shape dimorphism. Ultimate hypotheses (e.g. sexual selection, habitat partitioning) have been put forward to explain this variation, but proximate mechanisms operating during the juvenile stages remain largely unknown. Herein, we aim at elucidating the proximate mechanisms of sexual dimorphism in head and limb shape, performance and dewlap size in *Anolis baracoae*, a crown-giant anole. We used a longitudinal approach and raised 23 captive-bred juvenile *A. baracoae* lizards through adulthood. By quantifying body size, head and limb dimensions, dewlap size and bite performance, we obtained growth trajectories that were compared between the sexes and among traits. Our results show that the growth of head and limb shape is similar in males and females, whereas dewlap size and bite performance diverge at a specific age. Based on these results, we hypothesize that, whereas selection favors a similar head and limb shape in males and females, selection pressures on dewlap size and bite performance likely differ between the sexes. In addition, dewlap size starts diverging around the time the animals reach sexual maturity, whereas bite performance diverges much earlier in (sexually) immature males.

Introduction

Phenotypic differences between males and females have attracted the attention of evolutionary biologists for over a century (Darwin, 1871). Sexual dimorphism has been invoked as indicative of differential sexual and natural selection pressures, including inter- and intrasexual selective pressures, intersexual resource partitioning and/or different reproductive roles of males and females (Andersson, 1994; Losos, Butler & Schoener, 2003). Apart from shedding light on the ultimate causes of sexual dimorphism, however, our understanding of how and when the differences develop during ontogeny is essential to understand evolutionary patterns observed among adults (Badyaev, 2002; Cox & John-Alder, 2007; Howard, 2009). Sexual dimorphism can arise because of different growth trajectories in males and females before and after maturation, different size at birth and/or differential survival

or dispersal (Badyaev, Hill & Whittingham, 2001a; Badyaev, Whittingham & Hill, 2001b; Badyaev, 2002; Haenel & John-Alder, 2002). Intersexual differences in size at birth and in growth trajectories are typically caused by differences in developmental or physiological pathways (e.g. Cox & John-Alder, 2007). Differential survival and dispersal are linked to ecological factors that may also influence males and females differently (e.g. predation, competition; Badyaev *et al.*, 2001b). To complicate matters even further, sexual dimorphism can be plastic and the degree to which it is expressed often depends on environmental conditions, such as food availability, predation pressure, humidity and density (e.g. Madsen & Shine, 1993; Stamps, Losos & Andrews, 1997; Stamps, 1999; Bronikowski, 2000; LeGalliard *et al.*, 2006; Bonneaud *et al.*, in press). Because males and females may differ in their response to limiting resources, their growth rates may differ, potentially resulting in sexual size dimorphism at

adulthood (e.g. Niewiarowski & Roosenburg, 1993; Perry, 1996; Stamps *et al.*, 1997; Haenel & John-Alder, 2002; LeGalliard *et al.*, 2006; Lailvaux, Gilbert & Edwards, 2012).

Whereas most studies have compared growth patterns of a single trait, that is body size, between sexes of different species or populations, growth patterns may also differ between traits within a single individual (e.g. Humphrey, 1998; Badyaev *et al.*, 2001a,b; Howard, 2009) and between size and shape variables (Butler & Losos, 2002; Schwarzkopf, 2005; Kaliontzopoulou, Carretero & Llorente, 2008; Hasumi, 2010). Differences in growth patterns among traits result from differences in the allocation of energy toward each trait, which in turn depends on the immediate functional importance of the trait at a certain age. For instance, within one population of house finches, the heterochrony between body and bill traits seemed related to the onset of various life-history events, such as (early) fledging and self-feeding (Badyaev *et al.*, 2001a).

In this study, we document patterns of sexual dimorphism in body and limb dimensions, bite performance and dewlap size in an *Anolis* lizard. *Anolis* lizards are a textbook example of an adaptive radiation and the different ecomorphs – species which inhabit similar microhabitats and which resemble each other behaviorally and phenotypically – evolved independently on each of the bigger Caribbean islands (Losos & Chu, 1998; Losos *et al.*, 1998). It has been documented previously that ecomorphs vary in degree of adult sexual dimorphism in body size and shape (Butler, Schoener & Losos, 2000; Butler & Losos, 2002; Losos *et al.*, 2003; Butler, 2007), with microhabitat partitioning and sexual selection as the most likely candidate selective pressures explaining this variation (Butler *et al.*, 2000). The habitat hypothesis links habitat visibility to sexual size dimorphism in such a way that sexual size dimorphism is predicted to be greater in open (i.e. high visibility) habitats as intruders will more easily see the territory holder and will be more effectively deterred than in closed (i.e. low visibility) habitats (Butler *et al.*, 2000).

In addition, *Anolis* lizards are also sexually dimorphic in dewlap size (Losos *et al.*, 2003; Vanhooydonck *et al.*, 2005a; Johnson & Wade, 2010). Most *Anolis* species possess a dewlap, that is an extendable throat fan, which varies greatly in size, shape and pattern among species, populations or individuals (Vanhooydonck *et al.*, 2005a,b, 2009; Nicholson, Harmon & Losos, 2007). In most island species, females also possess a dewlap, but it is generally smaller and less frequently used during displays than in males (Johnson & Wade, 2010, but see Harrison & Poe, 2012). Although the function of the dewlap is still not fully understood, it has been shown to be an important signal during social inter- and intrasexual interactions. In addition, it may also serve as species recognition signal during encounters with congeners and as a pursuit deterrence signal in encounters with predators (e.g. Echelle, Echelle & Fitch, 1978; Fitch & Hillis, 1984; Losos & Chu, 1998; Leal, 1999; Jenssen, Orrell & Lovern, 2000; Lailvaux & Irschick, 2007; Nicholson *et al.*, 2007). Some ultimate hypotheses, such as sexual selection, species recognition or ecomorph convergence, have been put forward to explain the diversity in male dewlap design and dewlap dimorphism across *Anolis* species (Nicholson

et al., 2007; Harrison & Poe, 2012). However, the proximate mechanisms shaping the dewlap during ontogeny, driving sexual dimorphism in adult dewlap size, have not been elucidated. It is, however, known that the growth of the dewlap is maintained under conditions of dietary restriction in males (Lailvaux *et al.*, 2012).

In this study, we document the patterns in sexual dimorphism in shape, performance (bite force) and dewlap size in *Anolis baracoae*, a crown-giant anole from Cuba. The crown-giant ecomorph as a group has been previously shown to be dimorphic in both size and shape (Butler *et al.*, 2000; Butler & Losos, 2002; Losos *et al.*, 2003). We use a longitudinal approach and raised *A. baracoae* juveniles through adulthood under homogeneous laboratory conditions to avoid a potential differential response of males and females to limited resources (but see Lailvaux *et al.*, 2012). By quantifying body size, head and limb dimensions, dewlap size and bite performance at set time intervals, we determine whether growth trajectories differ between males and females, and if so, at what point in time the sexes diverge. In addition, we compare the growth trajectories of head and limb dimensions, which are generally to be thought of as naturally selected traits, with the growth trajectory of dewlap size, a primarily sexually selected trait, and bite performance (an ecologically relevant performance trait that is of crucial importance in male–male interactions and may allow individuals to increase their dietary breadth).

Material and methods

Study animals

We obtained 23 captive-bred juvenile and subadult *A. baracoae* ($N_{\text{males}} = 14$, $N_{\text{females}} = 9$) through a breeder in October 2007. These animals are the first and second generation offspring from wild caught, non-related adult individuals. Details on the breeding conditions are described in Holáňová & Hribal (2005). Upon arrival in the laboratory in Antwerp, the lizards were kept in individual cages ($h \times w \times d_{\text{small}} = 0.35 \times 0.60 \times 0.60$ m and $h \times w \times d_{\text{large}} = 1.00 \times 0.40 \times 0.60$ m) in a climate-controlled room with a day : night cycle of 10:14 h and room temperature set at 28°C. Each cage was equipped with a light bulb (8W), providing extra heat and light for 10 h per day, some branches and leaf litter scattered on the floor. We fed the lizards with calcium-dusted crickets, waxworms and banana twice a week. In addition to spraying the lizards three times a week, water was provided *ad libitum*.

Upon arrival in the laboratory, we measured bite force, body, head and limb dimensions of all individuals and took a digital picture of the dewlap for the first time (measurement 0; measurement details indicated in the succeeding text). Subsequently, these measurements were repeated 11 times at varying time intervals spanning a total of 3.5 years. Measurements 1–5 were taken at a 4-week interval; measurements 6–7 at a 6-week interval; measurements 8–10 at a 5–6-month interval and the last measurement 20 months after measurement 10.

Measurements

All measurements were carried out in a climate-controlled room set at 28°C during daytime hours.

We measured *in vivo* bite force for all individuals using an isometric Kistler force transducer (type 9203) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5995; see Herrel *et al.*, 1999 for a detailed description of the set-up). A lizard was taken from its cage and immediately induced to bite the force transducer by tapping it on the side of the mouth. The tapping typically resulted in a threat response in which the jaws are opened maximally. The free ends of the holder (bite plates) were then placed between the jaws, which resulted in prolonged biting. Each bite was scored as 'good' or 'bad' based on the willingness of the lizard to bite the plates and the vigor with which it bit. This was repeated five times in a row. As an estimate of maximal bite-force capacity, we used the highest bite force of the five bites for each individual. Because of logistical problems (i.e. unavailability of the set-up), we were unable to execute the third bite-force measurement, that is 8 weeks after the arrival of the animals in the laboratory.

Subsequent to the bite-force measurements, we took the following morphological measurements using digital calipers (Mitutoyo CD-15DC, Mitutoyo Europe GmbH, Neuss, Germany; accuracy of 0.01 mm) for each individual: snout-vent length (SVL), head length, femur length, tibia length, metatarsus length and length of longest toe of the hind foot. Head length was measured from the tip of the snout to the posterior edge of the parietal bone. We summed the four segments of the hind limb and used them as a measure of total hind limb length in subsequent analyses.

Lastly, we positioned the lizards sideways on a paper grid (grid cells = 10 mm × 10 mm) and pulled the base of the second ceratobranchial gently forward with a pair of forceps to obtain a measure of dewlap size. As the dewlap consists of a skin flap attached to the lizard's throat on the one side and to the hyoid bone on the other, the dewlap becomes maximally extended when the ceratobranchial is pulled forward completely (Font & Rome, 1990). After positioning the lizard in such a way that its extended dewlap was parallel to the lens (Tamron SP DI AF 90 mm; TAMRON Europe GmbH, Cologne, Germany) of the camera (Nikon D70S with a Sigma EM-140DG ring flash; Nikon Europe BV, Amsterdam, The Netherlands), we took a digital picture. Using the program

TPSDIG v1.40 (J. Rohlf, SUNY, Stonybrook, NY, USA), we digitized the outer edge of the dewlap and calculated total dewlap size for each individual. This method of measuring dewlap size yields highly repeatable results (Vanhooydonck *et al.*, 2005a).

Analyses

We compared the associations between the response variables dewlap size, head length, hind limb length and maximal bite force and the explanatory variable SVL between male and female lizards using mixed models. Both SVL and SVL² were added as continuous covariates (after centering on zero by subtracting mean SVL). Sex and the two-way interactions between sex and both SVL and SVL² were added to compare associations between males and females. To incorporate the repeated measures structure of the data in the analyses, we added individual and its interactions with SVL and SVL² as random effects. We used an analysis of variance (ANOVA) approach to test for the significance of the fixed effects and Satterthwait's method (lmerTest in R v. 2.15; free software to be downloaded from: <http://www.r-project.org/>) to determine the degrees of freedom. Parameter estimates and their statistical significance are reported and estimates are used to visualize the model fit in the graphs. Model fit was explored by testing normality of the residuals and inspecting associations between the fitted and residual values.

Results

ANOVA results, the parameter estimates and the statistical significance of the factors in the mixed models comparing the association between head length, hind limb length, dewlap size and maximal bite force with SVL between males and females are given in Tables 1 and 2. Most importantly, two interactions appeared to be statistically significant, suggesting a sexual growth dimorphism in dewlap size and bite force (Table 1). For head length and hind limb length, these interactions were not statistically significant, suggesting that growth in these traits is similar in males and females (Table 1, Fig. 1a and b).

For dewlap size, we found a difference in the quadratic term between males and females (significant SVL² × sex interaction, Table 2). In males, there was a slight, albeit not significant,

Table 1 Analysis of variance results for the mixed models comparing the associations between head length, hind limb length, dewlap size and bite performance with snout-vent length (SVL; centered around zero) between male and female *Anolis baracoae* lizards

Source	Head length	Hind limb length	Dewlap size	Bite performance
SVL	F_{1,67} = 17050***	F_{1,17} = 4046***	F_{1,17} = 324***	F_{1,21} = 123***
SVL ²	F _{1,41} = 0.10	F _{1,41} = 1.8	F _{1,26} = 0.14	F_{1,39} = 5.1*
Sex	F_{1,236} = 6.6*	F_{1,140} = 8.2**	F _{1,210} = 0.31	F_{1,191} = 17.6***
SVL × sex	F _{1,67} = 2.0	F _{1,17} = 0.0	F _{1,19} = 2.27	F_{1,21} = 6.9*
SVL ² × sex	F _{1,236} = 0.4	F _{1,140} = 1.2	F_{1,210} = 7.4**	F _{1,191} = 0.1

Asterisks refer to the level of significance (**P* < 0.05, ***P* < 0.01, ****P* < 0.001). Statistically significant effects are shown in bold.

Table 2 Overview of parameter estimates (\pm SE) and associated significance tests of the mixed models comparing the association between snout-vent length (SVL) and head length, hindlimb length, dewlap size and bite performance (centered around zero) between male and female *Anolis baracoae*

Effect	Head length	Hind limb length	Dewlap size	Bite performance
Intercept ^a	28.4 \pm 0.11***	62.2 \pm 0.40***	416 \pm 16***	11.1 \pm 0.60***
SVL ^a	0.31 \pm 0.003***	0.74 \pm 0.013***	10.6 \pm 0.70***	0.30 \pm 0.03***
SVL ^{2a}	-0.0002 \pm 0.0001	-0.0016 \pm 0.0005**	0.026 \pm 0.015	0.0026 \pm 0.0008**
Sex ^b	-0.07 \pm 0.17	-0.76 \pm 0.63	9.27 \pm 25.1	-2.13 \pm 0.95*
SVL \times sex ^c	-0.0064 \pm 0.0046	0.0042 \pm 0.020	-1.62 \pm 1.08	-0.12 \pm 0.04*
SVL ² \times sex ^c	-0.0001 \pm 0.0002	0.0010 \pm 0.0009	-0.07 \pm 0.025**	0.0004 \pm 0.0013

The bottom two rows provide tests for differences between males and females in the linear and quadratic terms, respectively (i.e. two-way interactions). Asterisks refer to the level of significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Parameter estimates significantly different from zero are shown in bold.

^aParameter estimate describing the association for males.

^bDifference in intercept between males and females.

^cDifference in slope between males and females.

positive quadratic effect of SVL, whereas in females the quadratic term was significantly smaller (negative difference in slopes, Table 1) and appeared to be significantly negative (slope = -0.04, SE = 0.02, $t = -2.04$, $P = 0.04$). A graphic exploration showed a very comparable increase of dewlap area with SVL for animals with SVL smaller than 100. When growing larger, however, the estimated curves diverged between males and females (Fig. 1c). In females, the growth after reaching a SVL of 100 mm was less pronounced compared with males, leading to a male biased sexual dimorphism in larger/older individuals (Fig. 1c).

For bite force, the linear term differed between males and females (significant SVL \times sex interaction, Table 2). In males, there was a slight, albeit not significant, negative linear effect of SVL, whereas in females the linear term was significantly smaller (negative difference in slopes, Table 2) and appeared to be significantly negative (slope = -0.29, SE = 0.12), $t = -2.40$, $P = 0.02$. A graphic exploration showed a very comparable increase of maximal bite force with SVL for animals with SVL smaller than 80 mm. When growing larger, however, the estimate curves diverged between males and females (Fig. 1d). In females, the increase in maximal bite force after reaching a SVL of 80 mm was less pronounced compared with males, leading to a male biased sexual dimorphism in larger/older individuals (Fig. 1d).

For all models, residuals did not show signs of deviations from normality (Shapiro Wilks' $W > 0.95$) and there were no associations between the fitted values and the residuals, suggesting appropriate model fit.

Discussion

Our results show differences between the sexes in the growth patterns of different traits in *A. baracoae*. Whereas head length and hind limb length grow in a similar fashion in males and females, dewlap size and bite performance diverge between males and females during growth. Even more so, the timing at which dewlap size and bite performance start diverging differs. Whereas growth in dewlap size is similar until the

animals reach a SVL of 100 mm, bite-force growth curves start diverging much earlier (i.e. at a SVL of 80 mm). No data on age or size at sexual maturity in *A. baracoae* lizards are currently available in the literature or from professional breeders. However, to estimate body size and age at sexual maturity of our animals, we made use of such data available for a wide range of *Anolis* species, including other crown-giants (Ruibal, Philibosian & Adkins, 1972; Andrews & Rand, 1974; Trivers, 1976; Stamps & Krishnan, 1997). Size at sexual maturity in *Anolis* lizards can be expressed as a proportion of maximum adult body size in males and females. Based on actual data of 33 *Anolis* species, the ratio of size at sexual maturity to maximum body size averages 0.73 (range: 0.68–0.81) in males and 0.77 (range: 0.64–0.82) in females (Stamps & Krishnan, 1997). Using the average ratio and maximum body size of *A. baracoae* as reported in Rodriguez-Schettino (1999; 150.4 mm in males, 135.5 mm in females), we estimate males reach sexual maturity at a SVL of 110.4 mm and females at 103.8 mm. Our results thus suggest that dewlap size diverges around the time the animals become sexually mature, whereas bite performance diverges already in (sexually) immature animals.

We hypothesize that the difference in timing of the sexual divergence in dewlap size and bite performance during growth may be related to a difference in the functional role of the two traits at a certain age (cf. Badyaev & Martin, 2000). For dewlap size, our data suggest the dewlap in males starts to grow faster than the dewlap in females around the time they reach sexual maturity. In *Anolis* lizards, dewlap extensions are part of the typical displays performed by males during fights with conspecific males, during interactions with females and in antipredator displays (Williams & Rand, 1977; Leal & Rodriguez-Robles, 1997a,b; Losos & Chu, 1998; Leal, 1999; Jenssen *et al.*, 2000; Tokarz, Paterson & McMann, 2003; Johnson & Wade, 2010). Females typically use dewlap extensions less frequently (Jenssen *et al.*, 2000; Orrell & Jenssen, 2003; Johnson & Wade, 2010), as do juveniles (Lovern & Jenssen, 2001). It can be expected that dewlap size is of high functional importance to male *A. baracoae* upon reaching

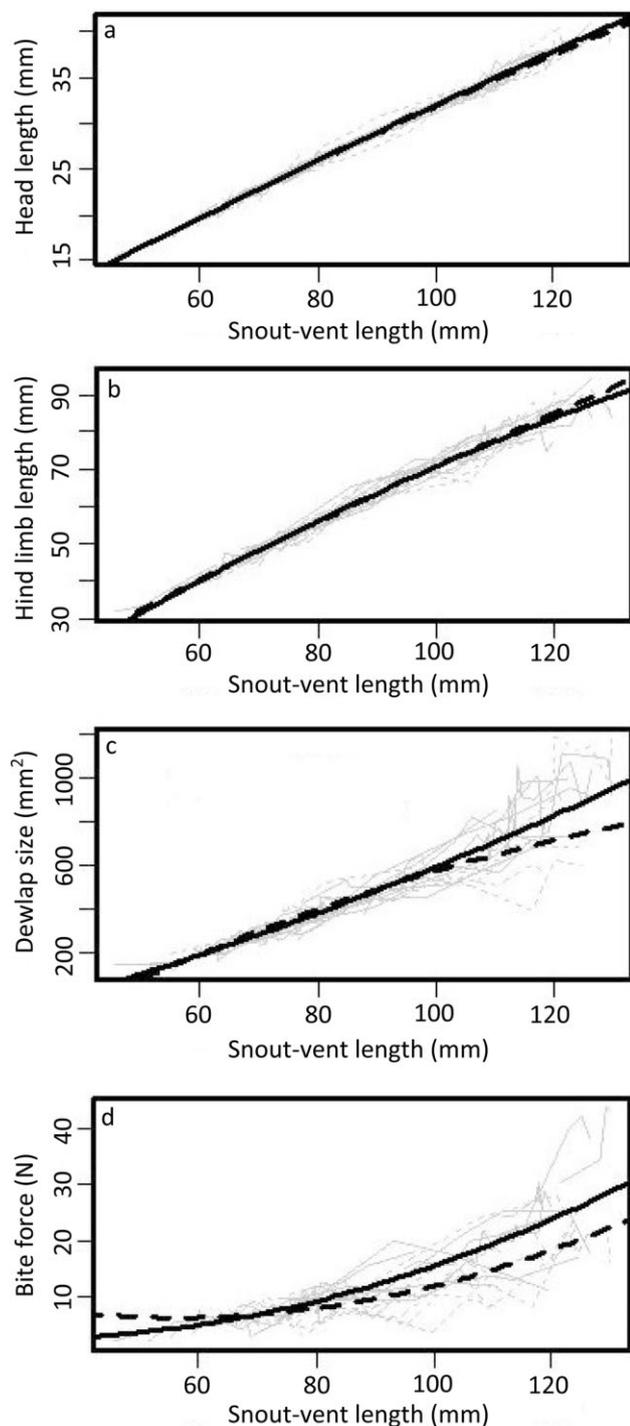


Figure 1 Association between snout-vent length (SVL) and head length (a), hind limb length (b), dewlap size (c) and bite performance (d) in *Anolis baracoae* males and females. Grey lines represent the individual-specific measurements. Estimates curves, based on a mixed model analysis (see text and Table 1 for details), are shown in black. Solid lines represent males, dashed lines females.

sexual maturity, as this may correspond to the point in a male's life when it becomes important to fight conspecifics and occupy high-quality territories. Possibly, displays which involve extending the dewlap are intense and crucial in males needing to gain access to a territory and/or to guard established territories from intruders imposing strong constraints on the growth of the dewlap at this point.

Bite performance, on the other hand, diverges when animals are still (sexually) immature. Based on our repeated SVL measurements, we estimate the delay between the divergence in dewlap size and bite performance to be between 6 to 12 months. Although it has been shown previously that dewlap size is a good predictor of bite performance (Vanhooydonck *et al.*, 2005a,b; Irschick *et al.*, 2006; Lailvaux & Irschick, 2007) and bite performance may determine fighting success in (some) male *Anolis* lizards (Lailvaux *et al.*, 2004; Lailvaux & Irschick, 2007), our findings do not corroborate the idea that bite performance is (solely) under sexual selection, at least not in *A. baracoae* lizards. On the contrary, our data suggest bite performance may be at least partly under natural selection given that bite force starts diverging before sexual maturity is reached in either sex. The divergence in bite performance early on (i.e. before reaching sexual maturity) may be related to a sexual difference in ecological factors, such as diet, to avoid intersexual competition over limited resources between subadult males and females (Schoener, 1967; Herrel *et al.*, 2006; Vanhooydonck *et al.*, 2010; Lopez-Darias *et al.*, in press). Because detailed ecological data are missing, we were unable to explicitly test this idea in this study.

Notably, the differences in growth of both dewlap size and bite performance occur without the influence of environmental factors, such as predation pressure and/or interindividual competition, as the animals were raised under identical laboratory conditions. Contrary to field studies that have shown that growth rates in males and females differ, resulting in sexual dimorphism at adulthood, because of a differential response to limiting resources (e.g. Niewiarowski & Roosenburg, 1993; Perry, 1996; Stamps *et al.*, 1997; Haenel & John-Alder, 2002, LeGalliard *et al.*, 2006) as well as laboratory studies showing that bite force is dependent on resource availability (Lailvaux *et al.*, 2012), this cannot be argued in this study. Instead, differential growth in the dewlap and bite performance appears to be 'intrinsic' to the animals and may be physiologically (e.g. hormonally) and/or genetically determined (Irschick *et al.*, 2006; Husak *et al.*, 2007).

Lastly, head length and hind limb length relative to body size (i.e. shape) grow in a similar way and at a similar speed in both male and female *A. baracoae*, suggesting that selection pressures favor similar trait expression in either sex (Howard, 2009). As in other ecomorphs, the degree of shape dimorphism (in adults) seems to be positively correlated to the variation in structural habitat (Butler & Losos, 2002; Losos *et al.*, 2003); our result suggests a very restrictive use of the available microhabitat by the two sexes in *A. baracoae*. In addition, Butler & Losos (2002) predicted a great limb shape dimorphism in crown-giant anoles because of the need for the highly territorial male anoles to display in open microhabitats, thus being more vulnerable to predation. They hypothesize that

high sprint speeds, and thus long limbs, are selected for under these circumstances in male crown-giant anoles. However, our data on *A. baracoae* do not corroborate this idea. Because quantitative data on microhabitat use and display behavior in this species, and crown-giants in general (see Losos *et al.*, 2003), are largely lacking, we are currently unable to explicitly test the validity of these hypotheses for the species under study. In addition, we cannot exclude the possibility that raising the animals under laboratory conditions in a predator- and competitor-free environment may have resulted in similar growth rates in head and limb dimensions in male and female *A. baracoae* whereas this may not have been the case in the wild.

In conclusion, growth patterns differ between the sexes and among traits in laboratory-raised *A. baracoae* lizards. The similar growth of head and limb shape possibly suggests that selection favors similar trait expression in males and females. The opposite is true for dewlap size and bite performance. Moreover, as dewlap size diverges around the time the animals reach sexual maturity, this suggests that dewlap size functions as a signal during intra- and intersexual interactions. Bite performance, on the other hand, starts diverging between males and females at a much earlier, that is the immature stage. This may suggest that bite performance is, at least partly, under natural selection with young males and females potentially already specializing on different food resources. We acknowledge, however, that based on the data presented in this study, we can only put forward evolutionary hypotheses without being able to test them. To actually test adaptive and/or selective explanations, data from field selection experiments and/or a comparative approach are needed.

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