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The relationship between dewlap size and performance changes with age and sex in a Green Anole (*Anolis carolinensis*) lizard population

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Abstract Ornaments are believed to signal an individual's ability to reproduce successfully and/or survive. Since an individual's fitness is often influenced by multiple traits (e.g. number of copulations, ability to acquire nest sites or to escape predators), which are difficult to quantify simultaneously, we examine performance traits (bite force, jumping performance) believed to be relevant to an individual's fitness. Specifically, we ask whether variation in dewlap size is related to variation in body size, bite force and jumping ability in the lizard *Anolis carolinensis*. Our results show that dewlap size is correlated with jumping capacity across all individuals, whereas the relationships between dewlap size, body size and bite force differ depending on sex/age class. We argue that selection against relatively large dewlaps at the transition between small mature and large mature males might be responsible for the lack of a relationship within large males. The absence or presence of a correlation between dewlap size and bite force, on the other hand, might be explained by differences in behaviour, such as territory establishment, anti-predator tactics, and/or

mate choice. Our work thus suggests that selective forces influencing the evolution of ornaments may operate differently on different sexes and life-history stages.

Keywords Ornaments · Selection · Performance · Intrapopulation differences

Introduction

Ever since Darwin proposed his theory of sexual selection (Darwin 1871), the evolution of ornaments has attracted the attention of evolutionary biologists. In general, ornaments are believed to mirror the intrinsic state of an organism as evidenced by numerous studies showing a link between variation in ornament design and variation in the ability to mate and/or survive (e.g. Møller 1988a; Veiga 1993; Grether 1996; Møller and Nielsen 1997; Forsman and Appelqvist 1999; Saino et al. 1997; Pryke et al. 2001; Kruuk et al. 2002; Ellers and Boggs 2003). For example, barn swallows with long and symmetric tails survive better than conspecifics with short, asymmetric tails (Møller and Nielsen 1997). Similarly, male damselflies with large wing spots are more successful at holding large territories and mate more frequently than the conspecifics with small wing spots (Grether 1996).

In most studies, ornament size or shape is correlated to a limited set of fitness components, such as the number of copulations, adult survival rate, the number of nest sites, or territory quality (e.g. Møller 1988b; Møller and Nielsen 1997; Pryke et al. 2001; Ellers and Boggs 2003). Critical to this approach are the assumptions that the co-variation between the trait under consideration and fitness does not differ among the various fitness components (e.g. survival, reproductive success) and that it persists throughout the entire life cycle (see Preziosi and Fairbairn 2000; Fairbairn and Reeve 2001; Gomez 2004). In many cases, however, ornaments might be correlated to multiple fitness components in different or even opposing ways and these relationships might vary for different sex and age classes (Blanco and De La Puente 2002).

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Anolis lizards are characterized by a conspicuous ornament, called a dewlap. The dewlap is an extendable throat fan that varies extensively in size, shape and colour among and within species (Echelle et al. 1978; Fitch and Hillis 1984; Losos and Chu 1998; Jenssen et al. 2000). In most *Anolis* species, both sexes possess a dewlap, although males typically have much larger dewlaps than females. Dewlap extensions are an important component of anoline display behaviour and are used in male–male, male–female and female–female contexts, as well as during encounters with predators (e.g. Williams and Rand 1977; Leal and Rodriguez-Robles 1997a, b; Losos and Chu 1998; Leal 1999; Jenssen et al. 2000; Tokarz et al. 2003). Display behaviour under various conditions has been well documented for *Anolis carolinensis* (Jenssen 1977; DeCourcy and Jenssen 1994; Nunez et al. 1997; Lovern et al. 1999; Jenssen et al. 2000; Lovern and Jenssen 2001; Orrell and Jenssen 2003). In *A. carolinensis*, different sex and age classes extend the dewlap under different circumstances. While male lizards extend their dewlap both during social interactions and in isolation (i.e. non-directed display), females extend their dewlap less frequently during encounters, and never in isolation (Orrell and Jenssen 2003). Juvenile behaviour resembles female behaviour in that juveniles never display in isolation, but only during agonistic interactions (Lovern and Jenssen 2001). Therefore, one might expect that different evolutionary pressures will act on dewlap size in male, female and juvenile *A. carolinensis* lizards, potentially resulting in different relationships among dewlap size and performance capacity (see Blanco and De La Puente 2002).

From a practical perspective, however, we cannot quantify all fitness (i.e. lifetime reproductive success) components simultaneously for all age and sex classes in natural populations of *A. carolinensis* lizards. Instead we measure the capacity to perform different tasks (e.g. biting, locomotor ability) that are believed to be relevant for an individual's fitness (e.g. biting for feeding or fighting, moving to escape from predators or defend territories; Arnold 1983; Garland and Losos 1994; Irschick and Garland 2001). Our aim is not to measure performance as a surrogate of fitness (Emerson and Arnold 1989). We quantify the ability to perform different functional tasks related to different components of fitness as a first step to an integrative approach of the study of the evolution (and constraint) of ornamental design (see also Arnold 1983; Garland and Losos 1994). Subsequently, it can be questioned whether differences in performance translate into differences in fighting ability, attractiveness, and ability to escape predators. In this study, we use bite force and locomotor performance as “ecologically relevant traits” for *A. carolinensis*.

Several lines of evidence suggest a strong link between bite force and fighting ability in *Anolis* lizards. In turn, fighting ability might influence fitness as it affects resource (e.g. territories, females) acquisition and defense against competitors. Behavioural observations indicate that during fights, *Anolis* males sometimes bite one another, employ jaw sparring and interlocking, and occasionally even slam the opposing lizard to the substrate (Greenberg and Noble

1944; McMann 1993; Stamps and Krishnan 1997, 1998; Jenssen et al. 2000). We can thus expect that individuals with high bite forces will be at an advantage in male–male contests. Recent work substantiates this idea; in staged encounters between large similarly sized male *A. carolinensis*, individuals with the highest bite forces won significantly more often (Lailvaux et al. 2004). Moreover, in other lizard species variation in bite force is tightly linked to variation in diet, and thus potential to survive (Verwajen et al. 2002).

Locomotor performance is also positively correlated to the ability of male lizards to establish social dominance in experimental arenas (Garland et al. 1990; Robson and Miles 2000; Perry et al. 2004). Furthermore, lizards in general, and green anoles in particular, frequently run and jump in nature, indicating the basic importance of locomotor performance to their lifestyle (Garland and Losos 1994; Irschick and Losos 1998).

We address the above issues by measuring performance (biting, jumping), and dewlap size in a large sample of *A. carolinensis* lizards. In addition, we specifically consider the role of body size in mediating the relationship between dewlap size and performance. We do so because body size is one of the most important factors determining fighting ability (review in Maynard et al. 2003), and because we compare different age classes which differ greatly in body size. We ask two primary questions with these data: (1) Does dewlap size correlate to body size and performance capacity in *A. carolinensis*? (2) Does the nature of the correlations change with sex and age?

Material and methods

Study species

We studied a population of *A. carolinensis* at Good Hope Field, a lowland swamp, in Southeastern Louisiana. In total, 403 lizards were captured by hand or noose between 23 September and 18 October 2002. We transported all animals to the lab at Tulane University, New Orleans. Since male *Anolis* lizards possess two enlarged anal scales and females do not, we could easily sex all individuals, including juveniles. Of the 403 individuals, 292 were males and 111 were females.

Measurement of dewlap size

To obtain a reliable measure of dewlap size, we positioned the lizard sideways and pulled the base of the second ceratobranchial gently forward with a pair of forceps. Since a dewlap consists of a skin flap attached to the lizard's throat on one side and to the hyoid bone on the other, the dewlap becomes maximally extended when the second ceratobranchial is pulled forward completely (see Bels 1990). Before taking a digital picture, we positioned the lizard in such a manner that the extended dewlap was parallel to the lens of the camera (Nikon Coolpix 4500). We digitized the outer edge of the dewlap using the program

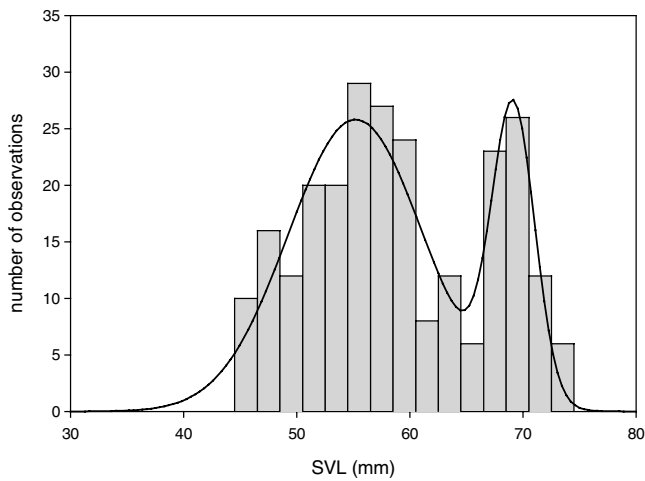


Fig. 1 Size distribution of adult male *A. carolinensis* individuals from a lowland swamp population in Southern Louisiana ($N=251$). Bars represent the observed frequency within each size class. The line represents the bimodal distribution based on the dip test (see text for details). A “dip” occurs at a SVL between 64 and 65 mm

TPSDIG (v 1.39; J. Rohlf, SUNY Stony Brook) and calculated the total dewlap area for each individual. This method of measuring dewlap size yields highly repeatable results (Vanhooydonck et al. 2005).

Size distribution

We measured the snout-vent length (SVL) of all individuals to the nearest 0.01 mm using digital calipers (Mitutoyo CD-15DC). In our sample, male SVL ranged from 24.17 to 73.71 mm. *A. carolinensis* lizards reach sexual maturity at SVL around 45 mm (Hamlett 1952). Of the 292 male individuals used in further analyses, 41 were sexually immature (i.e. <45 mm). The SVL distribution for mature males, however, departed significantly from unimodality (Hartigan 1985, Hartigan and Hartigan 1985; $N = 251$, dip statistic = 0.044, $p < 0.05$; Fig. 1), suggesting a bimodal distribution. The “dip” in the distribution is situated at a SVL between 64 and 65 mm. We use the lower limit (64 mm) to distinguish between the two adult subsets (see Lailvaux et al. 2004). Hereafter, mature males with $SVL < 64$ mm will be referred to as “small mature males”, and mature males with $SVL \geq 64$ mm will be referred to as “large mature males”.

Female SVL ranged from 25.65 to 59.43 mm; 50 female individuals were classified as sexually immature ($SVL < 45$ mm) and 61 as sexually mature ($SVL \geq 45$ mm). The SVL distribution of mature females did not depart from unimodality ($N=61$, dip statistic = 0.037, $p > 0.10$) and no adult subsets were defined.

Performance data

We were able to gather performance data on all study traits for 320 individuals ($N_{\text{males}}=235$; $N_{\text{females}}=85$).

Prior to experimentation, and in between all performance trials, individuals were placed for at least 1 h in an incubator set at 32°C , which falls within the range of field body temperatures of active *A. carolinensis* lizards (Clark and Kroll 1974). We measured bite force of all individuals upon arrival in the lab. The jumping trials were conducted the following day. All lizards were marked with a black paint mark on the belly prior to release to avoid collecting them more than once for the study. Lizards were released at the exact site of capture (based on GPS recordings and numbered flags) within 48 h of capture.

Bite force

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 detailed description of set-up). We induced the lizards to bite the force transducer by tapping them softly on the side of the mouth. The tapping readily resulted in a characteristic threat response where the jaws are opened maximally. The free ends of the holder, i.e. the bite plates, were then placed between the jaws, which immediately resulted in fierce and prolonged biting. We scored each bite as “good” or “poor”. “Good” trials were those in which the animals readily bit the plates. “Poor” trials were eliminated from the analyses. As an estimate of maximal bite capacity, we used the highest bite force out of the five bites for each individual.

Jumping performance

We used a custom built force plate ($30 \text{ cm} \times 18 \text{ cm} \times 1 \text{ cm}$, length \times width \times height) to measure the three-dimensional ground reaction forces during jumping. The output of the strain gauges was sent to a 12-bridge, 8-channel amplifier (K, N Scientific) and subsequently A-D converted at 10 kHz (Instrunet, model 100B). Digital traces were read into a G4 MacIntosh computer using Superscope (GW Instruments). Force traces were smoothed using a low-pass filter before further analysis. The acceleration of the centre of mass was obtained by dividing the resultant ground reaction force by the body mass of the animal. Numerical integration of the acceleration profile yielded the instantaneous velocity of the centre of mass (integration constant set to zero). The displacement of the centre of mass was obtained by numerical integration of the instantaneous velocity during take-off. The angle of take-off was determined using the horizontal and vertical ground reaction forces during jumping. From these traces, we extracted peak instantaneous acceleration and velocity. Using the take-off angle (θ), the take-off velocity (V_i), and the horizontal displacement of the centre of mass during take-off (D_h), we calculated the horizontal jump distance as $D = D_h + D_a + D_f$, where D_f is the horizontal distance traveled from take-off height back to resting height, and D_a is the distance travelled during the ballistic phase of jumping [$D_a = (V_i^2 \sin 2\theta) / g$; see Toro et al. 2003 and references therein].

All animals were induced to jump from the edge of the force plate to a horizontal branch, positioned just outside the presumed maximal reach of each individual. We tried to elicit maximal effort by startling the animals using sudden hand clapping and/or waving or by tapping the tail slightly (only for adults). We only included trials in which the lizards jumped from a standstill, with their four feet on the force plate, and when the tap on the tail did not coincide with take-off. All animals underwent three to five jumping sessions, each at least 1 h apart. We scored all jumps as “good” or “poor”. “Good” trials were those in which the lizards readily jumped when placed on the platform; only these trials were retained for analysis. For each individual, at least three jumps that fulfilled all of our criteria were obtained. As an estimate of maximum acceleration, maximum velocity and jump distance, we used the highest peak acceleration, highest peak velocity and the largest distance, respectively, as measured over all jump trials (for each individual).

Statistical analyses

Prior to statistical analyses, SVL, dewlap size and the four performance variables (i.e. bite force, jump distance, acceleration and velocity) were logarithmically (\log_{10}) transformed. We performed two sets of analysis of co-variance (ANCOVA). First, to determine whether the relationship between dewlap size versus body size (SVL) and all performance variables differed between sex/age classes, we performed an ANCOVA with SVL, or one of performance variables as the dependent variable, sex and age class as fixed factors, and dewlap size as the co-variate. If the interaction between sex or age class and dewlap size was significant, we performed bi-variate regressions (SVL or one of the performance variables as the dependent variable and dewlap size as the independent variable) per sex/age class. If the interaction effect was non-significant, we pooled all the data in the regression analysis.

Second, to determine whether the relationship between SVL and the performance variables differed among sex/age classes, we performed an ANCOVA with the performance variable (i.e. bite force, jump distance, velocity or acceleration) as the dependent variable, sex and age class as fixed factors and SVL as the co-variate. If the interaction between sex or age class and SVL was significant, we performed bi-variate regressions (performance variable as the dependent variable and SVL as the independent variable) per sex/age class. If the interaction effect was non-significant, we pooled all the data in the regression analysis.

Results

Dewlap size, body size and performance

The relationship between dewlap size and body size (SVL) differed significantly among sex/age classes (ANCOVA, both interaction effects $F > 3.89$, $p < 0.05$). Subsequent bi-variate regressions per class showed that the variation in dewlap size explained a significant proportion of the variation in body size within four out of the five groups (i.e. immature males, small mature males, immature females, mature females, Table 1, Fig. 2). However, within large mature males, dewlap size and body size are not correlated (Table 1, Fig. 2).

The relationship between dewlap size and bite force differed among age classes (ANCOVA, dewlap size \times age class, $F_{2,311} = 6.70$, $p = 0.001$). We subsequently performed bi-variate regressions of bite force against dewlap size for each sex/age class separately. The variation in dewlap size explained a significant proportion of the variation in bite force within immature males, small mature (SM) males and immature females (Table 1, Fig. 3). In large mature (LM) males and mature females, on the other hand, no significant correlation existed between dewlap size and bite force (Table 1, Fig. 3).

For all three jumping performance variables (jump distance, velocity and acceleration), the relationship with

Table 1 Summary of regression analyses

<i>y</i>	<i>x</i>	Age	Sex	<i>df</i>	<i>r</i>	<i>F</i>	<i>p</i>	<i>a</i>	<i>b</i>
SVL	Dewlap size	IM	M	1, 27	0.87	85.56	<0.0001	0.35	1.05
		SM	M	1, 142	0.75	177.72	<0.0001	0.39	1.04
		LM	M	1, 59	0.15	1.26	0.27	0.05	1.74
		IM	F	1, 34	0.84	79.22	<0.0001	0.57	0.73
		MA	F	1, 47	0.42	9.87	<0.0001	0.22	1.37
Bite force	Dewlap size	IM	M	1, 27	0.66	20.89	<0.0001	0.61	-0.86
		SM	M	1, 142	0.70	136.86	<0.0001	1.36	-1.97
		LM	M	1, 59	0.02	0.02	0.90	-0.03	0.88
		IM	F	1, 34	0.82	72.01	<0.0001	1.21	-1.67
		MA	F	1, 47	0.20	1.86	0.18	0.25	-0.02
Bite force	SVL	IM	M	1, 27	0.69	24.02	<0.0001	1.61	-2.47
		SM	M	1, 143	0.89	537.56	<0.0001	3.30	-5.29
		LM	M	1, 59	0.32	6.88	0.011	1.64	-2.18
		IM	F	1, 34	0.89	123.55	<0.0001	1.89	-2.87
		MA	F	1, 47	0.64	31.76	<0.0001	1.50	-2.21

Regression parameters are given per sex/age class. Regression equation is of the form $\log(y) = a + b \log(x)$

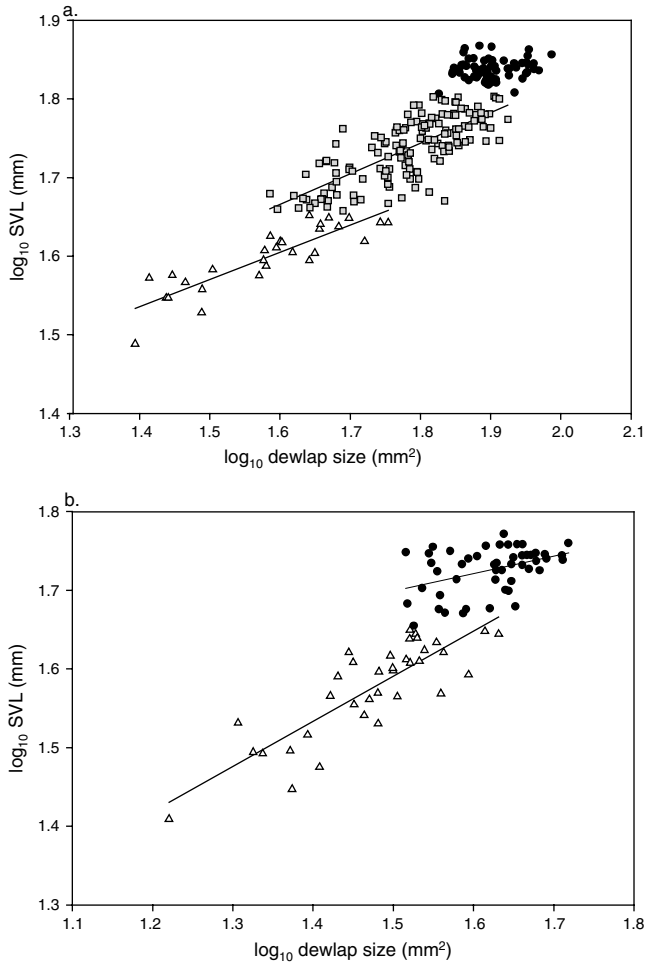


Fig. 2 Plots of SVL against dewlap size in *A. carolinensis*. **a** Males. Symbols and colours refer to the three age classes (Δ : immature; \blacksquare : small mature; \bullet : large mature). **b** Females. Symbols and colours refer to the two age classes (Δ : immature; \bullet : mature)

dewlap size was similar for all sex/age classes (ANCOVA, all interaction effects $p > 0.10$) so we pooled all the data in the regression analysis. Across all individuals, the variation in dewlap size explained a significant proportion of the variation in jump distance, velocity and acceleration (Table 2, Fig. 4).

Body size and performance

Only for bite force, did the relationship with SVL differ among sex/age classes (ANCOVA, both interaction effects

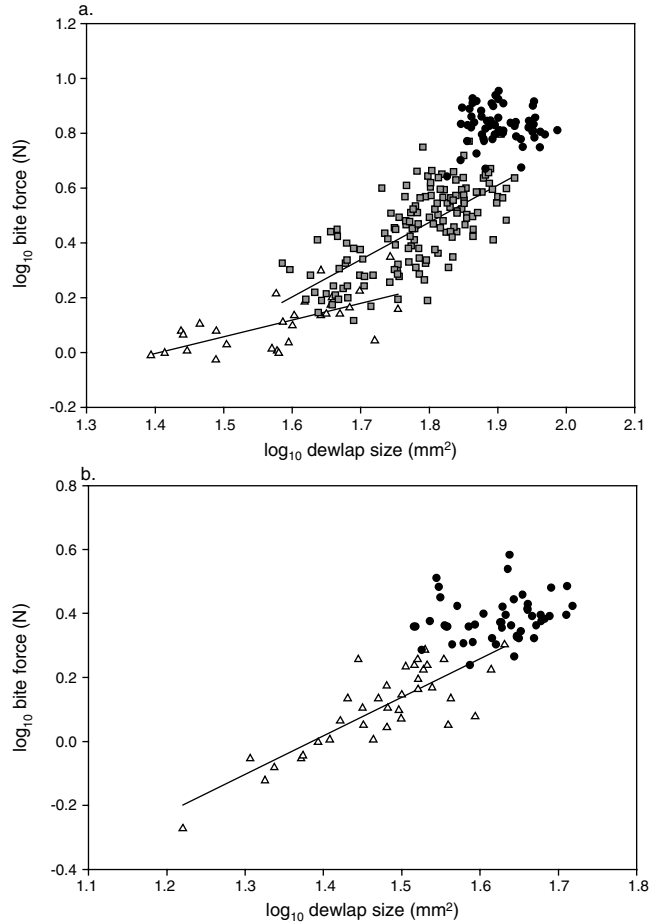


Fig. 3 Plots of bite force against dewlap size in *A. carolinensis*. **a** Males. Symbols and colours refer to the three age classes (Δ : immature; \blacksquare : small mature; \bullet : large mature). **b** Females. Symbols and colours refer to the two age classes (Δ : immature; \bullet : mature)

$F > 7.00$, $p < 0.004$). Subsequent regression analyses were performed for each class separately. Within all five sex/age classes the variation in SVL explained a significant proportion of the variation in bite force, but the slope of the regression within small mature males was much greater than that within the other classes (Table 1).

The relationships between SVL and all three jumping performance variables were similar for all sex/age classes (ANCOVA, all interaction effects $F < 3.36$, $p > 0.07$) so all the data were pooled in the subsequent regression analysis. Across all individuals, the variation in SVL explained a significant proportion of the variation in jump distance, velocity and acceleration (Table 2).

Table 2 Summary of regression analyses

Regression parameters are for pooling data of all individuals. Regression equation is of the form $\log(y) = a + b \log(x)$

<i>y</i>	<i>x</i>	<i>df</i>	<i>r</i>	<i>F</i>	<i>p</i>	<i>a</i>	<i>b</i>
Distance	Dewlap size	1, 317	0.68	274.36	<0.0001	0.53	-1.58
Velocity		1, 314	0.66	239.03	<0.0001	0.25	-0.30
Acceleration		1, 317	0.39	55.28	<0.0001	0.13	1.24
Distance	SVL	1, 318	0.78	485.43	<0.0001	1.04	-2.46
Velocity		1, 315	0.76	416.8	<0.0001	0.49	-0.71
Acceleration		1, 318	0.46	84.39	<0.0001	0.27	1.00

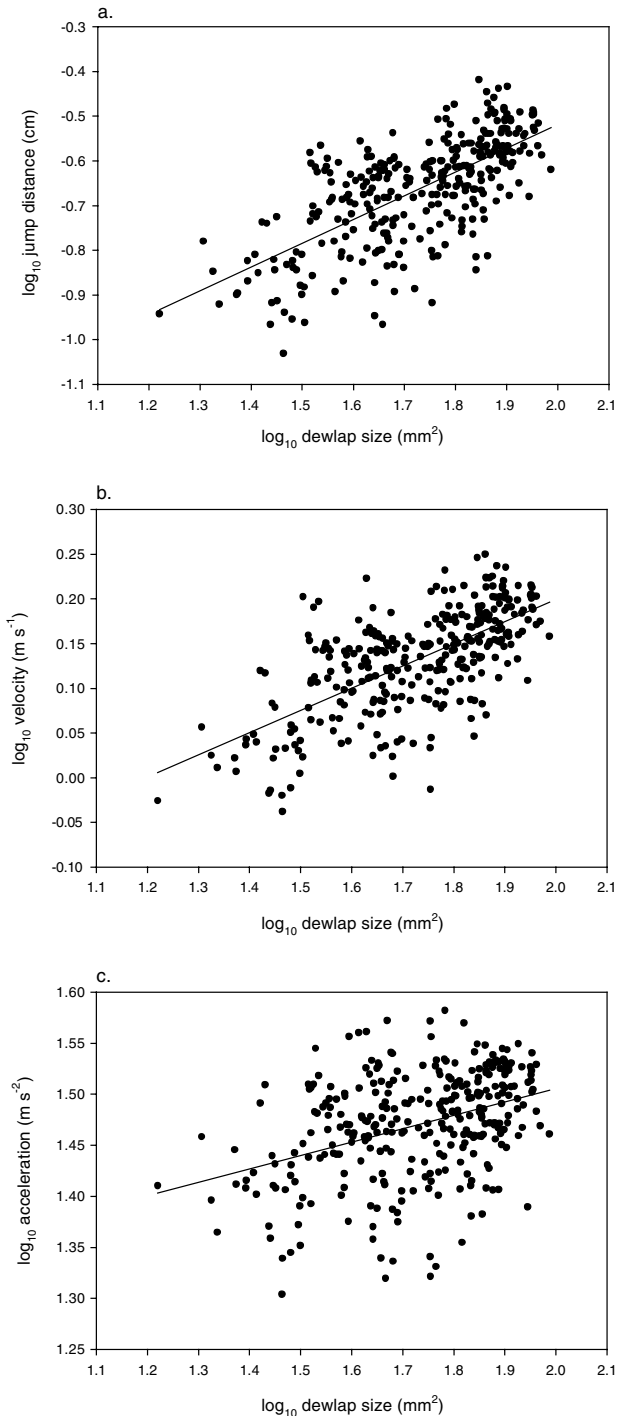


Fig. 4 Plots of jumping performance variables against dewlap size in *A. carolinensis* (all data pooled). **a** Jump distance against dewlap size. **b** Velocity against dewlap size. **c** Acceleration against dewlap size

Discussion

Dewlap size, body size and bite force

Dewlap size is correlated with body size and bite force in some sex/age classes of *A. carolinensis* but not in others.

In small mature males and juveniles (of either sex), dewlap size is positively correlated with body size and bite force, suggesting that dewlap size might indicate overall size and bite strength in these sex/age classes. Within mature females and large mature males the relationships between dewlap size, body size and bite force are less self-evident. In mature females, dewlap size indicates body size but not bite strength, whereas dewlap size in large mature males is not correlated with overall size or bite performance.

Large mature males

The fact that the differences in dewlap size within large mature males do not correspond to differences in body size suggests that dewlap size is constrained or selected against in the largest *A. carolinensis*. This in turn might weaken the overall relationship between dewlap size and bite force. Our data (see Fig. 2 and Table 1), suggests that increases in dewlap area diminish dramatically within large mature males as size increases (see Echelle et al. 1978 for an interspecific comparison). Therefore, either the ontogenetic growth trajectory of the dewlap does not coincide with the indeterminate growth of other structures (e.g. head), or males with relatively large dewlaps are selectively removed from the population. Assuming that small mature males and large mature males represent two age classes (see Lailvaux et al. 2004), the relative proportions of small mature to large mature males in this population (177:74) indicates that most of the small mature males never survive to the large mature stage. This result indeed suggests that intense selection is operating on this stage of the life cycle.

We tested this idea of selection on (relative) dewlap size in *A. carolinensis*, by calculating two selection differentials (Endler 1986). One quantity, i , is a measure of directional selection, the other, j , is a measure of stabilizing (if negative) or disruptive selection (if positive). The quantities i and j measure the proportional change in the mean and variance, respectively (Endler 1986). We calculated these differentials for residual (against SVL) dewlap size. Comparing relative dewlap size between small mature and large mature males showed that both quantities, i and j , were significantly negative ($i = -0.36$, $t_{203} = -2.48$, $p = 0.014$ and $j = -0.46$, $F_{145, 58} = 1.84$, $p = 0.0043$, respectively), thus suggesting both directional and stabilizing selection on (relative) dewlap size (see appendix). Given this directional selection, small mature males with relatively large dewlaps are selected against when entering the transition stage to large mature males. Stabilizing selection, on the other hand, causes individuals with extremely small and extremely large dewlaps to be selectively removed from the population. Of course, this analysis is not as powerful as field analysis of marked animals through time, but it nonetheless suggests that the optimum dewlap size is a compromise between counteracting selective pressures (e.g. sexual and natural selection; see also Echelle et al. 1978). The fact that the expression of ornaments is often reduced in environments where the predation rate is high substantiates this idea (see Stone et al. 2003 and references therein).

Mature females

In mature females, dewlap size indicates body size but not bite strength. Because dewlap size and body size are correlated, the lack of a relationship between dewlap size and bite force cannot be explained by selection against large dewlaps in mature females (cf. large mature males). Behavioural observations, however, show that females use their dewlap rarely in a consensual context, and not at all in a heterosexual context (Jenssen et al. 2000; Lovern and Jenssen 2001). Moreover, females do not, unlike adult males, extend their dewlap in isolation (Lovern and Jenssen 2001), nor as part of a ritualized combat scheme (McMann 1993; Jenssen et al. 2000). Also mature female *A. carolinensis* have relatively stable, small, overlapping, and lightly defended home ranges, thus engaging infrequently in aggressive interactions (Orrell and Jenssen 2003). The lack of correlation between dewlap size and bite force in adult females might thus be explained by the fact that the dewlap conveys different (or no) information in this age/sex class. Similarly, cheek patches convey different kinds of information in male and female great tits. Whereas cheek patch immaculateness is correlated to timing of breeding in females, immaculate males rear heavier chicks (Ferns and Hinsley 2004).

Small mature males and juveniles

Within small mature males and juveniles of both sexes, dewlap size is an indicator of size and of bite strength. In addition, similar increases in body size in small and large mature males result in a much greater increase in bite force in the former than in the latter class. This finding suggests that high bite force is selected for in small mature males.

We believe that in small mature males and in juveniles, being able to convey information on one's size and bite force without having to engage in a physical combat might be advantageous in different, non-mutually exclusive contexts. First, behavioural observations on male *A. carolinensis* lizards show that they engage in fierce fighting (with conspecifics) over territories, using chases, jaw-sparring and sometimes biting techniques (Greenberg and Noble 1944; McMann 1993; Stamps and Krishnan 1997, 1998; Jenssen et al. 2000; Orrell and Jenssen 2003). In doing so, they might sustain serious injury or die through their higher susceptibility to predators (Stamps 1983). Because juveniles defend (immediate and future) resources, such as suitable habitat for foraging, thermoregulation, or eventual breeding (i.e. prospective resource hypothesis; Lovern and Jenssen 2001), the same situation might apply within this age class. Second, dewlap extensions are known to be an effective pursuit-deterrent signal in some *Anolis* species; snake predators are less likely to pursue lizards that are dewlapping (Leal and Rodriguez-Robles 1995, 1997a, b; Leal 1999). By displaying, a potential prey is believed to communicate to the predator that it has been detected, thus lowering the predator's chances for a successful attack (i.e. pursuit deterrent hypothesis; Leal and Rodriguez-Robles

1997b). In addition, the dewlap may function as a direct signal of the prey's chances at outrunning an attack because the intensity of signaling (e.g. number of pushups, dewlap extensions) is positively correlated to endurance capacity (Leal 1999). Because small individuals may be more susceptible to predation than large individuals (cf. small individuals are worse at jumping than large individuals), it might pay to advertise high "vigor" or ability to escape when one is small. In addition, the dewlap may function as an important signal used in a female choice context (Crews 1975, Andrews 1985). Possibly, young (small) males may need to signal much more than old males that are established territory owners. Data on female choice, however, are needed to test this hypothesis.

Dewlap size and jumping performance

We found no significant effect of sex/age class on the relationship between dewlap size and any of the three jumping performance variables; across all classes, dewlap size is positively correlated to jump distance, velocity, and acceleration. In addition, an individual's ability at all three jumping traits increases with body size. Therefore, individuals with large dewlaps are greater in size and are better jumpers than those with smaller dewlaps. In lizards, locomotor capacity has been shown to be important in different contexts, such as predator-prey and/or intraspecific interactions (e.g. Garland et al. 1990; Garland and Losos 1994; Robson and Miles 2000; Vanhooydonck and Van Damme 2003, Perry et al. 2004). More specifically, *Anolis* lizards frequently run and jump when escaping predators (Losos and Irschick 1996; Irschick and Losos 1998) or when feeding (Irschick and Losos 1998). Moreover, locomotor performance (i.e. sprint speed and endurance) appears to be correlated to social dominance in *Anolis cristatellus* (Perry et al. 2004) and within male *A. carolinensis* better jumpers are more likely to win fights (Lailvaux et al. 2004). The fact that jumping capacity in *A. carolinensis* seems to be both under natural and/or sexual selection in all sex/age classes might explain why we found an overall relationship between dewlap size and jumping performance. We note however that the exact nature of the selective process might differ among sex/age classes.

Conclusions

Our data suggest that the dewlap in *A. carolinensis* is likely to be a visual cue of body size, bite strength and/or jumping capacity. The relationship between dewlap size, body size and bite performance, however, changes with age and sex. These differences can be explained in different ways. In large mature males, counteracting selective pressures on dewlap size most likely explain the absence of a correlation. In the other sex/age classes, the absence or presence of a correlation between dewlap size and bite force might be explained by the relative importance of the dewlap during conspecific conflicts, predatory attacks, and/or for mate

choice. Our work thus suggests that selective forces influencing the evolution of ornaments may operate differently on different sex/age classes.

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Appendix

Directional selection, quantity i , is calculated using Eq. 1; stabilizing (if negative) and disruptive selection (if positive), both quantity j , are calculated using Eq. 2 (Endler 1986).

$$i = \frac{\bar{x}_a - \bar{x}_b}{\sqrt{v_b}} \quad (1)$$

$$j = \frac{v_a - v_b}{v_b} \quad (2)$$

where \bar{x}_a is the mean value in trait \times after selection; \bar{x}_b the mean value in trait \times before selection; v_a the variance in trait \times after selection; v_b the variance in trait \times before selection.

The statistical significance of directional selection, i , is tested using Eq. 3; the statistical significance of stabilizing or disruptive selection, j , is tested using Eq. 4 (Endler 1986).

$$t_{(n-2)} = \frac{\bar{x}_a - \bar{x}_b}{\sqrt{n[(N_b - 1)v_b + (N_a - 1)v_a]/(n - 2)N_b N_a}} \quad (3)$$

$$F_{(N_b, N_a)} = \frac{v_b}{v_a} \quad \text{or} \quad F_{(N_a, N_b)} = \frac{v_a}{v_b} \quad (\text{whichever is larger}) \quad (4)$$

where N_a is the sample size after selection; N_b the sample size before selection; and $N = N_a + N_b$.

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