Does dewlap size predict male bite performance in Jamaican *Anolis* lizards?

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Summary

1. The theory of the evolution of secondary sexual traits through male–male competition is based on the assumption that these traits are reliable cues for an animal's fighting capacity. In this paper, we test whether a secondary sexual trait, dewlap size, is an honest predictor of bite strength in *Anolis* lizards. Since male anoles will bite one another during territorial fights, bite performance may play an important role in determining the outcome of male–male fights.

2. We measured dewlap size and bite force in a size series of adult males of three Jamaican anoles, i.e. *Anolis grahami* Gray 1845, *A. lineatopus* Gray 1840 and *A. valencienni* Duméril & Bibron 1837.

3. In both *A. grahami* and *A. lineatopus*, males with relatively large dewlaps tend to bite relatively harder, while the relationship between relative dewlap size and bite force was clearly non-significant within the twig anole *A. valencienni*.

4. Our results thus suggest that dewlap size is an indicator of relative bite force in the former two species, but not in the latter. We argue that interspecific variation in territorial behaviour might explain this difference.

Key-words: Honest signalling, lizards, sexual selection

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Introduction

Secondary sexual traits evolve through the process of sexual selection, either via female choice, male–male competition or a combination of both (see Berglund, Bisazza & Pilastro 1996). In the context of male–male competition, secondary sexual traits are used as signals, which may function as reliable cues for a male's overall robustness and/or fighting ability (Berglund *et al.* 1996). To determine whether a signal is honest with regard to a male's quality or social status, researchers typically test whether a link exists between the variation in the design (i.e. size, shape, coloration) of secondary sexual traits (e.g. antlers, plumage) and the variation in the ability to reproduce successfully and/or win fights with other males (e.g. Backwell & Passmore 1996; Jennions & Backwell 1996; Candolin 1999; Backwell *et al.* 2000). Relatively few studies, however, have measured whether the size or shape of a secondary sexual structure is related to ecologically relevant performance capacities, particularly those that are directly related to fighting

ability (see Brandt 2003; Perry *et al*. 2004). This is surprising since studies of performance (e.g. bite performance, locomotor endurance) offer an excellent opportunity for testing whether male signals are honest indicators of a male's 'quality', as measured by their ability to perform ecologically relevant tasks. Moreover, rendering inferences between signal design and performance are an excellent complement to typical male–male combat studies.

In this study, we examine variation in a secondary sexual trait, i.e. dewlap size, in three species of Jamaican *Anolis* lizards. *Anolis* lizards are characterized by the possession of an extensible throat fan, or dewlap. There is extensive variation in dewlap size and colour among and within *Anolis* species (Echelle, Echelle & Fitch 1978; Fitch & Hillis 1984; Losos & Chu 1998; Jenssen, Orrell & Lovern 2000) and dewlap expansions appear to be an important component of the anoline display behaviour in various contexts. In aggressive male–male interactions, the dewlap is believed to represent a 'threat' or 'challenge' to potential intruders (Greenberg & Noble 1944; Jenssen *et al*. 2000); females, on the other hand, appear to choose males based on dewlap characteristics and are more receptive towards males that are performing dewlap extensions (Greenberg & Noble 1944; Crews 1975). Finally, in a predator–prey context

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the dewlap seems to act as a pursuit-deterrent signal as snakes stop moving towards dewlapping male anoles (Leal & Rodriguez-Robles 1997a,Leal & Rodriguez-Robles 1997b; Leal 1999). However, no studies have examined whether the relative size of the dewlap is an honest indicator of fighting ability, or one of its components (e.g. bite performance).

Several lines of evidence indicate a strong link between relative (i.e. size-adjusted) bite force and male–male fighting ability in lizards. First, *Anolis* lizard males will bite one another during fights, sometimes even slam one another against the substrate during physical combat (Greenberg & Noble 1944; McMann 1993; Stamps & Krishnan 1997, 1998; Jenssen *et al*. 2000). Thus, one would expect that individual anole males with relatively high bite forces would possess an advantage during male–male contests relative to similarly sized anole males with relatively weak bite forces. Recent work verifies this assumption, showing that, during staged male–male contests, large *A. carolinensis* males with relatively high bite forces won significantly more fights against similarly sized males with relatively weak bite forces (Lailvaux *et al*. 2004). Second, several studies have shown a direct link between relative head size (which is typically proportional to relative bite force in lizards; Herrel *et al*. 1999; Herrel *et al*. 2001) and the ability to win male–male contests, or acquire high-quality territories (Hews 1990; Pratt *et al*. 1992; Molina-Borja *et al*. 1998; Gvozdik & Van Damme 2003; Perry *et al*. 2004). In short, a compelling body of evidence indicates that individual male lizards with enhanced biting abilities are at a competitive advantage for winning fights with other males.

We measured bite force and dewlap size in a size series of adult males of *A. lineatopus* Gray 1840, *A. grahami* Gray 1845 and *A. valencienni* Duméril & Bibron 1837 at a single lowland scrub forest locality in north-eastern Jamaica. The three species differ dramatically in morphological shape (e.g. limb, tail dimensions; Losos 1990), display behaviour (e.g. percentage time spent displaying; Losos 1990; Irschick & Losos 1996) and territoriality (Hicks & Trivers 1983; Irschick & Losos 1996). Nevertheless, the three species are similarly sized, and syntopic, thus offering an excellent point of comparison. Within each species, we tested whether relative dewlap size accurately predicts relative bite force, thus constituting an honest signal.

Materials and methods

STUDY ANIMALS

Adult individuals of three species of *Anolis* lizards were caught by noose or hand at the Discovery Bay Marine Laboratory (DBML), Discovery Bay, Jamaica, between 21 January 2002 and 2 February 2002. In total, we captured 11 adult male *A. grahami*, 31 adult male *A. lineatopus* and 13 adult male *A. valencienni*. Head length (HL) of all individuals was measured from the tip of the snout to the posterior edge of the parietal scale

using digital callipers (Mitutoyo CD-15DC, Mitutoyo (UK) Ltd, Telford, UK; precision 0·01 mm). Measurements of bite force and dewlap size were completed at the DBML field station on the same or following day the lizards were caught; after experimentation, all lizards were released at the same site where they had been caught.

MEASUREMENT OF BITE CAPACITY

We measured 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, Kistler Inc., Winterthur, Switzerland; 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. As body temperature is known to affect performance capacity in lizards, we placed the lizards outside (in the shade) in individual bags at least half an hour prior to experimentation and in between trials. In doing so, the lizards attained body temperatures equal or close to the environmental temperature, which approximated 30 °C. Because these three species occur sympatrically, and do not clearly differ in their microclimatic preferences (Schoener & Schoener 1971), it is reasonable to examine bite force at the same ambient temperatures for each species. We scored each bite as 'good' or 'poor'. '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.

MEASUREMENT OF DEWLAP SIZE

To measure dewlap size, we positioned the lizard sideways and pulled the base of the ceratobranchial, near its articulation with the basihyoid, gently forward with a pair of forceps. Since a 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. We then positioned the lizard in such a manner that the extended dewlap was laid flat on a piece of paper. We traced the outer edge of the dewlap with a pencil (scale 1:1). Afterwards, the drawings were digitized using the Scion Image for Windows software (v4·0.2; Scion Corporation 2000, Frederick, MD) and dewlap size was quantified for each individual. To determine whether this method yields a reliable estimate of dewlap size, we drew and digitized the dewlaps of five individuals twice and calculated the repeatability of our measurement (Lessells & Boag 1987). Repeatability proved to be very high ($r = 0·90$, $F_{1,4} = 44·67$, $P < 0·0001$).

ANALYSES

All data on HL, bite force and dewlap size were logarithmically ($\log_{10}$) transformed prior to statistical analyses. All statistical analyses were done using SPSS v.11·5 (SPSS Inc., Chicago, IL).

To test whether absolute dewlap size is a good predictor of absolute bite force, we regressed $\log_{10}$ bite force against $\log_{10}$ dewlap size using ordinary linear least-squares regression. To remove the effects of overall size on the dewlap size–bite force relationship, we regressed $\log_{10}$ bite force and $\log_{10}$ dewlap size against $\log_{10}$ HL and calculated the residual values for all individuals. We then regressed residual bite force (dependent variable) against residual dewlap size (independent variable). All of these regression analyses were done within each species.

Results

The regression of absolute bite force *vs* absolute dewlap size was significant within all three *Anolis* species (*A. grahami*: $r = 0.93$, $F_{1,9} = 55.66$, $P < 0.0001$; *A. lineatopus*: $r = 0.90$; $F_{1,29} = 126.05$, $P < 0.0001$; *A. valencienni*: $r = 0.87$, $F_{1,11} = 35.01$, $P < 0.0001$). Thus, absolute dewlap size is a good predictor of absolute bite force in all three species.

The regression of relative bite force against relative dewlap size, on the other hand, was significant within *A. lineatopus* ($r = 0.47$, $F_{1,29} = 8.39$, $P = 0.007$; Fig. 1a) and *A. grahami* ($r = 0.80$, $F_{1,9} = 16.28$, $P = 0.003$; Fig. 1b). The former significant relationships suggest that for a given body size, males with larger dewlaps bite harder in *A. lineatopus* and *A. grahami*. The regression of relative bite force against relative dewlap size was clearly non-significant within the remaining species, *A. valencienni* ($r = 0.08$, $F_{1,11} = 0.07$, $P = 0.79$; Fig. 1c). Thus, relative dewlap size is not a good predictor of relative bite capacity within *A. valencienni*.

Discussion

PERFORMANCE AND THE EVOLUTION OF HONEST SIGNALLING

Our results show that absolute dewlap size is a good predictor of absolute bite force in all three Jamaican species. After removing the effects of body size, however, the correlation between dewlap size and bite force remained significant within *A. lineatopus*, and *A. grahami*. Thus, in *A. lineatopus* and in *A. grahami*, males with large dewlaps, for their body size, tend to bite relatively hard. Thus, our results provide evidence that within at least two species of *Anolis* relative dewlap size is an honest predictor of an individual's fighting capacity as indicated by bite performance. In a similar fashion, display rate appears to indicate endurance capacity in other lizard species, i.e. *Uta stansburiana* (Brandt 2003) and *A. cristatellus* (Perry *et al*. 2004).
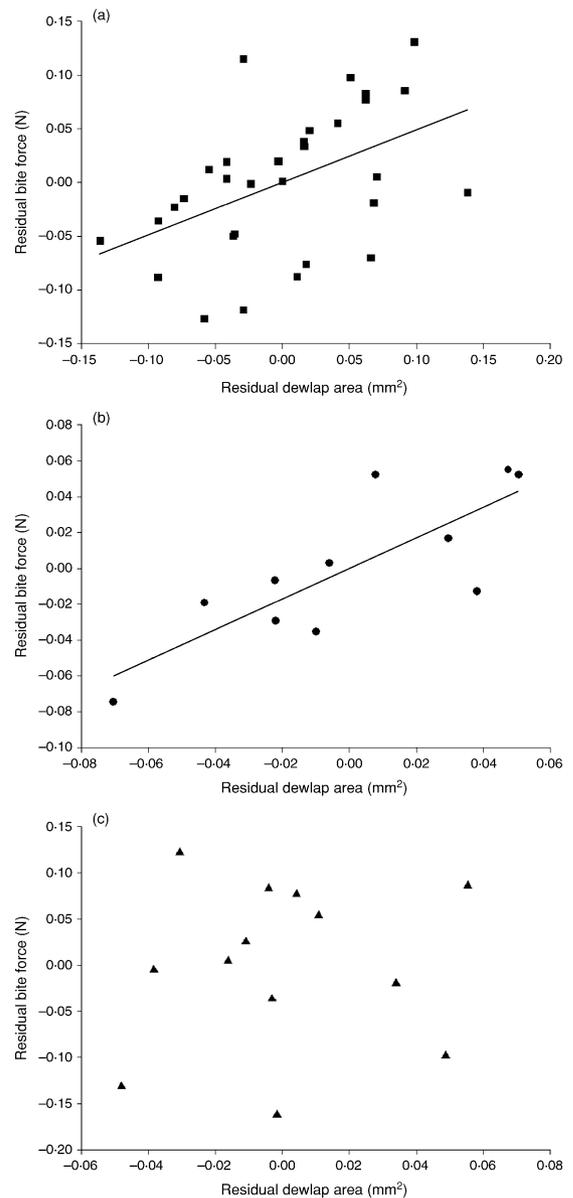
Fig. 1. Residual bite force *vs* residual dewlap size for three *Anolis* species: (a) residual bite force is positively correlated to residual dewlap size in *A. lineatopus* ($r = 0.47$, $P = 0.007$); (b) residual bite force is significantly correlated to residual dewlap size in *A. grahami* ($r = 0.80$, $P = 0.003$); (c) residual bite force is not correlated to residual dewlap size in *A. valencienni* ($r = 0.08$, $P = 0.79$).

By contrast, within the twig anole *A. valencienni* there was no apparent relationship between relative dewlap size and relative bite force. The fact that the dewlap seems to represent a signal in *A. lineatopus* and *A. grahami*, but not in *A. valencienni* might be explained by differences in the degree of territoriality. Both *A. lineatopus* and *A. grahami* are territorial anoles (Schoener & Schoener 1971). Territorial male anoles are known to aggressively defend their territories from intruders by using visual displays, including dewlap extensions. Thus, our data suggest that *A. lineatopus* and *A. grahami* males that bite relatively hard will also enjoy enhanced success in male–male encounters, although future studies

that test this possibility explicitly would be useful. If true, then bite force should be subject to sexual selection via male–male competition. On the other extreme, *A. valencienni*, a twig anole, is far less territorial (Hicks & Trivers 1983; Irschick & Losos 1996). This species is highly arboreal and cryptic, and males display less frequently (Irschick & Losos 1996). Further, male *A. valencienni* overlap in their home ranges substantially (Hicks & Trivers 1983). *Anolis valencienni* males therefore might not rely on biting during male–male encounters to the same extent as *A. lineatopus* and *A. grahami*. Thus, a coupling between dewlap size and bite capacity may not have evolved within *A. valencienni*, because males of this species may not engage in physical combat to the same extent *as A. lineatopus* and *A. grahami*.

It is important to note, however, that the dewlap is a multipurpose signal structure that is used for displaying to rival males, but also to potential mates, and predators (Leal & Rodríguez-Robles 1997a,b; Leal 1999). For example, detailed studies with the Puerto Rican anoles *A. cuvieri* and *A. cristatellus* show that during staged encounters with a model snake predator, male anoles displayed their dewlaps vigorously, and such vigorous displays appeared to be effective in deterring some attacks. These studies also reveal, however, that bite force could be important as a defensive mechanism against predators, as anoles would often bite and struggle when captured by snakes (Leal & Rodríguez-Robles 1995). Thus, the size of the dewlap may also have evolved as a signal to warn predators that anoles have powerful bites. Consequently, dewlap size in *Anolis* lizards has likely evolved in response to multiple ecological pressures (female attraction, male–male competition, and antipredator signalling; Greenberg & Noble 1944; Crews 1975; Leal & Rodríguez-Robles 1997a,b; Losos & Chu 1998; Leal 1999; Jenssen *et al.* 2000).

Even though we found a significant correlation between dewlap size and bite force, at least in some species, we note that the role of dewlap size in sexual selection is still not well understood. In *A. sagrei*, for instance, males do not display differently from conspecific males with or without (surgically removed) dewlaps, suggesting limited functional significance of the display of a male's dewlap during male–male interactions (Tokarz, Paterson & McMann 2003). While these results do not give information about the role of the dewlap in other contexts (e.g. predator encounters, female attraction; see above), it is true that dewlap traits besides size (e.g. colour, shape, movement) and different components of display behaviour (e.g. display rate, display repertoire) might (also) be indicators of performance in *Anolis* lizards.

Similarly, factors other than relative bite force may also be important for predicting whether male lizards will win or lose territorial fights. For example, previous studies have shown that locomotor performance is also an important determinant of male dominance in lizards (Garland, Hankins & Huey 1990; Robson &

Miles 2000; Perry *et al*. 2004). Indeed, while we argue that relative bite force is an important aspect of male fighting capacity in lizards, we do not exclude other possibly covarying factors.

Conclusions

We show that the size of a secondary sexual trait (dewlap size) is linked with a relevant aspect of fighting capacity (bite force) in territorial *Anolis* species, but not in non-territorial anoles. Our results suggest that dewlap size is sexually selected for through male–male territorial competition, and might serve as a visual cue to a male's fighting ability. It would be interesting to study whether similar relationships between secondary sexual traits (e.g. crests, horns, throat and body coloration, colour patches) and performance exist in other lizard groups.

Acknowledgements

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