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The Evolution of Performance-Based Male Fighting Ability in Caribbean *Anolis* Lizards

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ABSTRACT: Despite the empirical and theoretical attention paid to the role of sexual signals in resolving agonistic interactions between conspecific males, few studies have applied a comparative perspective, particularly across species that vary in combat intensity. We investigated the relative roles of a male sexual signal (dewlap size) and whole-organism performance capacity (bite force) on male combat outcomes in nine species of Caribbean *Anolis* lizards that differ markedly in territoriality, as indicated by sexual size dimorphism. We found that (1) dewlap size was generally an honest signal of bite force in dimorphic but not less dimorphic species; (2) maximum bite force consistently predicted male combat success in dimorphic but not less dimorphic species; (3) in contrast to a priori predictions, dewlap size significantly predicted male combat success in less dimorphic but not dimorphic species; and (4) the incidence of biting but not dewlapping increases as species become more dimorphic. These findings suggest that more dimorphic (and hence more territorial) species escalate to biting during fights more readily compared with less territorial species. The ecological and behavioral qualities of species may therefore modify both the shape and the size of sexually selected traits as well as the nature of the information those traits convey.

Keywords: bite force, dewlap, *Anolis*, territoriality, male combat, performance.

Sexual selection has equipped the males of many animal species with elaborate secondary sexual traits that function as signals or weapons during fights over access to females or resources that females require (Andersson 1994; Shuster and Wade 2003). Male signals and displays are thought to communicate information on fighting ability or resource holding potential (RHP) to rivals (Andersson 1994), and hence males often evaluate these signals to assess asymmetries in RHP between themselves and opponents during male-male combat (Jennions and Backwell 1996; Emlen 1997; Panhuis and Wilkinson 1999). Significant attention has been paid to the mechanisms by which conspecific males resolve agonistic interactions and the role that sexual signals play in such assessment games (Maynard Smith and Harper 2003; Stuart-Fox 2006). Classic models such as the sequential assessment game, based primarily on territorial species, posit that animals undergo a series of escalations, beginning with signaling and nonviolent display behaviors and concluding with sometimes violent and potentially damaging interactions (e.g., Parker 1974; Jenssen et al. 2005). However, animal species vary in the degree to which they actually proceed through these stages, with many species never reaching the final, most violent stage, whereas other species regularly fight intensely, sometimes with severe consequences (e.g., Bean and Cook 2001). Because of the complex nature of such ritualized assessment games, understanding the factors that influence fighting success requires an integrative approach that examines the relative size and shape of sexual signals as well as aspects of male RHP that might enable males to win the most violent stage of ritualized assessment (Stuart-Fox 2006).

In regard to more physical aspects of fighting, a growing literature demonstrates that whole-organism performance abilities (i.e., the capacity of an organism to conduct ecologically relevant tasks, such as running, jumping, or biting; Bennett and Huey 1990; Garland and Losos 1994; Irschick and Garland 2001) can influence male-male contests in various taxa, independent of body size, such that good performers typically win fights against poor performers (Lailvaux and Irschick 2006*a*). Male lizards, for example, will bite each other during fights, often causing severe injuries (Cooper and Vitt 1987; Jennings and Thompson 1999), and the ability to acquire or defend

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territories appears to be positively related to both relative bite force (Huyghe et al. 2005; Lappin and Husak 2005) and relative head size (correlated with bite force; Hews 1990; Herrel et al. 2001*a*, 2001*b*; Perry et al. 2004; but see Lappin and Husak 2005) in lizards. Furthermore, performance capacities important to fighting ability, such as bite force or endurance, are positively correlated, independent of body size, with the expression of male secondary sexual characters used during fights in several highly sexually dimorphic animal species (Lailvaux et al. 2005; Vanhooydonck et al. 2005*a*, 2005*b*), suggesting that male signals or displays may act as size-free indexes of important physiological components of fighting ability to rival males (Maynard Smith and Harper 2003).

Our primary goal in this article is to understand how two key factors in sexual selection, male sexual signal size (throat fan or dewlap size) and male fighting capacity (bite force), influence the outcome of male fights across a diversity of lizard species that vary in degree of territoriality. We emphasize that these two factors are not necessarily alternatives for dictating the outcome of male fights but rather may each be important at different stages of the fighting process and may therefore hold different significance for different kinds of species. For example, in species that rely primarily on ritualized assessment of signals and that rarely escalate to violent fights, the relative size of sexual signals and the manner in which they are used may be key dictators of fight success. By comparison, for species that regularly engage in violent fights, both signal size and performance may be relevant, especially if the signal itself is an honest signal of potentially damaging male fighting capacity or RHP. Examples abound in the literature of animals using signals that transmit information on potentially damaging male fighting capacity to avoid injury or death during fights (Andersson 1994).

We take an evolutionary approach to understanding the roles of sexual signal size and performance in dictating the outcome of male fights (Ord et al. 2001; Emlen et al. 2005; see also Lailvaux and Irschick 2006*a*). In contrast to male fighting, for which relatively few comparative data exist, the application of comparative methods to female choice has proved informative for understanding the evolution of male ornaments in several animal groups (e.g., Basolo 1996; Garcia and Ramirez 2005). Comparative studies of male combat could likewise yield crucial insights into the role of performance in dictating male fighting success, as animal species vary in both the frequency and the intensity of male-male contests (Shuster and Wade 2003; Lailvaux and Irschick 2006*a*). Hence, one might predict strong selection for performance capacities related to fighting ability (as well as morphological or behavioral indexes of such capacities) in some species but not others. For instance, in species in which males aggressively defend territories, males that can patrol territories more effectively (Andersson 1994), endure prolonged fights (Briffa and Elwood 2001, 2004), or inflict damage on opponents (Lailvaux et al. 2004; Huyghe et al. 2005; Husak et al. 2006) would likely be more effective at excluding rivals from their territories than would low-performance males. Conversely, performance abilities such as bite force may be less important for males of species that do not actively defend specific home ranges or that do not otherwise experience intense male-male competition (Vanhooydonck et al. 2005*a*).

An ideal system for examining evolutionary relationships among male signal size, performance, and male combat success would be one exhibiting independent evolution of species experiencing high and low levels of male competition. Caribbean *Anolis* lizards fit these criteria closely. *Anolis* is one of the most diverse vertebrate genera, having radiated into several morphologically and ecologically distinct forms (ecomorphs) that exhibit varying degrees of territoriality and male-male competition (Losos 1994; Roughgarden 1995; Irschick et al. 1997). This is evidenced by the remarkable diversity in sexual size dimorphism (SSD) among anole species, with some species exhibiting no SSD and other species having males with about twice the body length of females (Stamps et al. 1997; Butler et al. 2000). Previous authors have posited, with some support, a positive evolutionary relationship between SSD and the intensity of male-male competition across various animal taxa (for general discussions, see Andersson 1994; Blanckenhorn 2005). Stamps et al. (1997) also demonstrated a significant relationship among anole species between SSD and population density, therefore supporting the general view that the intensity of male competition and SSD are linked.

A second feature of anole diversity is the high degree of size variation in the dewlap, or throat fan (an exaggerated male trait in most species of sexually dimorphic anoles; Nicholson et al. 2007). Males display their dewlaps in several ecological contexts, including predator-prey interactions (Leal and Rodriguez-Robles 1995, 1997; Leal 1999) and male contests (Greenberg and Noble 1944; Rand and Williams 1970; Losos and Chu 1998; Jenssen et al. 2000), but little is known about the type of information conveyed by such displays or whether dewlaps serve similar signaling functions in different anole species. In a study of Jamaican *Anolis* lizards, Vanhooydonck et al. (2005*a*) found that residual (size-corrected) bite force is positively correlated with residual male dewlap size in two highly sexually dimorphic anole species but not in a less dimorphic one. A similar relationship between dewlap size and bite force also exists in the sexually dimorphic *A. carolinensis* (Vanhooydonck et al. 2005*b*; Irschick et al. 2006). Therefore, the dewlap might be a key index of male per-

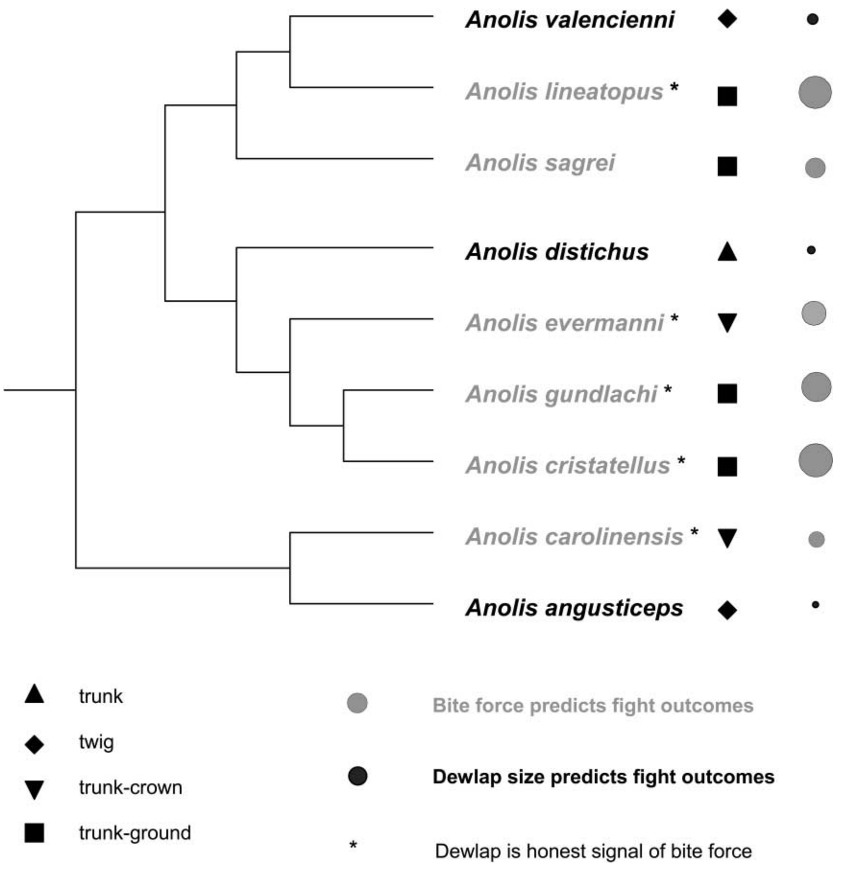

Figure 1: Phylogenetic relationships among *Anolis* species used in this study (based on Nicholson et al. 2005). Log sexual size dimorphism is proportional to circle diameters (data from Stamps et al. 1997; Butler et al. 2000). Symbols indicate ecomorph types; black and gray indicate fight outcome predictors. Species where dewlaps honestly signal information about bite force are marked with an asterisk. A color version of this figure is available in the online edition of the *American Naturalist*.

formance capacity in anoles experiencing intense male competition but not in species subject to lower levels of male competition (but see Tokarz et al. 2003). However, despite this work, no studies have taken a comprehensive evolutionary approach toward understanding the relative roles of dewlap size and bite force in influencing male combat success across a diversity of anole species.

We examined nine anole species that vary markedly in morphology, bite force, dewlap size, and SSD. We used SSD as a surrogate for the intensity of territorial behavior across these different species, as in prior work (see Shine 1989; Butler et al. 2000). The nine anole species comprise three independent radiations (Puerto Rican, Jamaican, and Cuban [i.e., Bahamas]) and four ecomorph types (trunk-ground, trunk-crown, twig, and trunk), spanning a range of social systems from conspicuous, abundant, and highly territorial (e.g., highly dimorphic trunk-ground ecomorphs such as *A. lineatopus*; Rand 1967; Butler et al. 2000) to cryptic, relatively scarce, and less territorial (e.g., monomorphic twig ecomorphs such as *A. valencienni*; Hicks and Trivers 1983) species (fig. 1). The evolution of dimorphic and less dimorphic species has occurred repeatedly within *Anolis* lizards (Butler et al. 2000), providing enhanced statistical power for elucidating relationships among armament size, performance, and male combat success.

We tested several predictions regarding the influences of bite force and sexual signal (dewlap) size on male combat success in these different anole species. (1) Sexual signal size will be a significant predictor (i.e., honest signal) of male fighting capacity (bite force) in territorial (high-SSD) but not less territorial (low-SSD or nonexistent SSD) species. (2) Maximum bite force will predict combat success in high-SSD but not lower-SSD species. (3) Sexual signal size will predict combat success in high-SSD but not lower-SSD species. (4) The incidences of biting and dewlapping during fights increase as species become more dimorphic (higher SSD) and hence more territorial.

To test these predictions, we collected the following data sets. First, we tested whether, within each species, the relative size of the dewlap was an honest signal of male bite force (sensu Vanhooydonck et al. 2005*a*, 2005*b*; Irschick et al. 2006). We focused on bite force because recent studies have provided evidence that biting generally, and bite force specifically, is important for resolving male-male territorial disputes in lizards (Lailvaux and Irschick 2006*a* and references therein). Second, we conducted experimental intraspecific male-male combat trials to determine the influence of bite force and dewlap size on combat success within each species. Finally, we conducted phylogenetically controlled analyses of fight data across all species to determine whether the frequency of biting, head bobbing, and dewlapping during fights increases or decreases with SSD (i.e., as males become larger than females and fights become more frequent and intense).

Methods

Sampling of Species

We sampled a total of 413 lizards comprising eight *Anolis* species from three Caribbean islands (Jamaica; South Bimini, Bahamas; and Puerto Rico) and one from the mainland United States (nine species total). We captured *A. lineatopus* and *A. valencienni* between June 3 and June 24, 2004, in the forests surrounding the Discovery Bay Marine Laboratory in Discovery Bay, St. Anne's Parish, Jamaica; *A. sagrei*, *A. distichus*, and *A. angusticeps* between July 25 and August 19, 2005, on South Bimini Island, Bahamas; and *A. evermanni*, *A. cristatellus*, and *A. gundlachi* in and around the El Verde field station in Puerto Rico between July 14 and August 1, 2006. All species were captured either by hand or by noose, and location of capture was noted to prevent staging experimental interactions between neighbors. Bite force data for *A. carolinensis*, obtained from a previous study using an identical protocol (Lailvaux et al. 2004), are included in this article for comparative purposes. Note, however, that the dewlap data for *A. carolinensis* (drawn from the same individuals used for bite force in Lailvaux et al. 2004), have not been published previously. All *A. carolinensis* combat trials were conducted in the spring of 2003. For all species, morphology and bite force were measured on the day of capture, and combat trials were carried out the day after. All lizards were marked and released at the point of capture within 48 h of combat trials.

Bite Force

We measured in vivo bite force for all individuals using an isometric Kistler force transducer (type 9023, Kistler, Wintherthur, Switzerland) connected to a Kistler charge amplifier (type 5058a; for detailed descriptions, see Herrel et al. 2001*a*, 2001*b*) and using standard methods. Briefly, we induced the lizards to bite forcefully on the free ends of the transducer (i.e., the bite plates) by placing the bite plates between the lizards' open jaws. Consistent with previous studies (e.g., Herrel et al. 2001*a*, 2001*b*; Lailvaux et al. 2004; Huyghe et al. 2005; Vanhooydonck et al. 2005*a*, 2005*b*; Irschick et al. 2006; Lailvaux and Irschick 2006*b*), bite trials were repeated five times for each individual, with a 30-min rest between trials. This methodology has been shown to be effective for eliciting maximum biting force in a wide variety of lizard species (see the above articles for more discussion on this topic, including the issues of motivation, etc.). Room temperature was a constant 29°C, and we used a Cox Technologies K-type digital thermometer (DE-305) to measure lizard body temperature (T_b) before each bite force measurement to ensure that all lizards were at the same T_b for each trial. This temperature is similar to shaded ambient air temperatures in the anole habitat (D. Irschick, personal observation) and is comparable with temperatures used in other studies of performance in these and other anole species (Lailvaux et al. 2004; Toro et al. 2004). The largest of an individual's five bite force measurements was taken to be the maximum bite force for that individual.

Dewlap Size

To determine dewlap area, we positioned the lizard sideways along a tabletop and gently pulled the ceratobranchial forward, near the articulation with the basihyoid, thus fully extending the dewlap. Extended dewlaps were photographed using a Sony DSC-P32 Cybershot digital camera mounted on a tripod, and the resulting images were digitized using tpsDig, version 1.3.1. This method yields repeatable results in other *Anolis* species (Vanhooydonck et al. 2005*a*, 2005*b*).

Morphology

We measured snout-vent length (SVL) for each individual lizard by using Mitutoyo digital calipers (±0.01 mm). Additionally, we also measured head length for each individual lizard, both as an additional proxy of body size and because head length is correlated with bite force in other lizard species (Herrel et al. 2001*a*, 2001*b*).

Male Combat Trials

We conducted male combat trials using methods consistent with previous studies (Lailvaux et al. 2004; Perry et al. 2004). Because body size can affect dominance in lizards

(Rand 1967; Hews 1990; McMann 1993) and because we were interested in factors that affect the outcome of male fights, independent of body size (for discussion of asymmetries and size matching in male contests, see Brandt 1999), males chosen for combat trials were matched for body size (SVL) to within 3 mm of each other (Lailvaux et al. 2004; Perry et al. 2004; see also Rand 1967). Following Perry et al. (2004), we did not include lizards with recently damaged tails in any combat trials because dominance status is also affected by tail loss (e.g., Fox et al. 1990; Martín and Salvador 1993). Each lizard was tested once.

Two size-matched males of the same species were introduced simultaneously into opposite ends of a 30 × 50 × 30-cm wire mesh enclosure containing a single perch beneath a suspended 75-W heat lamp. This cage design was chosen both to be consistent with Lailvaux et al.'s (2004) previous study on *A. carolinensis* and to facilitate interactions between males. One lizard of each pair was marked with a small spot of neutral white acrylic paint on the dorsal tail base for identification (as in Lailvaux et al. 2004; Jenssen et al. 2005), and the individual to be marked from each pair was determined by coin toss. The marked male was used as the focal male for logistic regression analysis. Each cage was then observed from the time of introduction for 1–6 h until resolution was reached. This longer observation period was required because although the majority of fights were resolved within the first 30 min to 1 h, in the case of low-SSD species such as *A. valencienni*, some interactions were less intense and tended to last for a longer period of time (note that our conclusions are unchanged whether or not our analyses are confined to the first 30 min of combat). To exclude observer effects, all trials were watched from a "hide" within the experimental room—S. P. Lailvaux stood behind a blind and observed the combat trials through the slats.

We determined winner/loser status based on a range of behaviors observed during the interaction period (for details, see Lailvaux et al. 2004). Aggressive behaviors (based on identifications in McMann 1993; Leal and Rodriguez-Robles 1995, 1997) received positive scores, and submissive behaviors received negative scores (Lailvaux et al. 2004; Perry et al. 2004). Bobbing displays and dewlap extensions received a weight of 0.5, while lateral displays, chasing, and biting an opponent each received a weight of 1. Crouching and escape behaviors earned a score of −1. At the end of each trial, a total score was given to each individual, and the lizard with the highest score in each dyad was considered the "winner." If no interactions were observed within the first 3 h of a trial, then that trial was excluded from the subsequent analyses (*A. carolinensis*, $N = 4$; *A. lineatopus*, $N = 4$; *A. valencienni*, $N = 3$; *A. angusticeps*, $N = 1$), and those individual lizards were not used again. Ultimately, we used 20 *A. angusticeps*, 22 *A. distichus*, 17 *A. valencienni*, 19 *A. carolinensis*, 24 *A. sagrei*, 24 *A. evermanni*, 18 *A. gundlachi*, 21 *A. lineatopus*, and 22 *A. cristatellus* pairs with clear resolutions in the final analyses. Thus, sample sizes for bite/dewlap regressions and male combat trials are different for several species, as males used in combat trials were a subset of those used in regression analyses.

Ethical Note

All experiments were carried out in accordance with an approved animal use protocol (IACUC 0189-2-16-0301), and male combat protocols were also approved by the U.S. Forestry Service under research permit CNF-2080. No animals were injured during male combat trials or at any other stage of this study.

Statistical Analyses

Test of Honest Signaling. Previous studies have shown that dewlap size predicts bite force in the territorial *A. lineatopus* and *A. carolinensis* but not in the nonterritorial *A. valencienni* (Vanhooydonck et al. 2005*a*, 2005*b*; Irschick et al. 2006). To test whether dewlap size predicts bite force in the other six species in our group (*A. angusticeps*, *A. distichus*, *A. sagrei*, *A. evermanni*, *A. gundlachi*, and *A. cristatellus*), we carried out regressions for each species with bite force as a dependent variable and dewlap size as an independent variable, following Vanhooydonck et al. (2005*a*). To assess relationships between bite force and dewlap size independent of overall body size, we regressed dewlap size and bite force against head length to calculate the residuals for each individual and then regressed residual dewlap size against residual bite force (consistent with Vanhooydonck et al. 2005*a*). Each regression was done separately for each species. Before analyses, variables were $\log_{10}$ transformed as required to meet linear regression assumptions of normality and homoscedascity. Successes of transformations were confirmed using Lilliefors tests.

Tests of Dewlap Size and Bite Force on Male Competition. We analyzed the effect of bite force, dewlap size, and head length on male combat outcomes for each species by using multiple logistic regressions. For the logistic regressions, one male in each trial was randomly chosen as a focal male (see "Male Combat Trials"). If the focal male was a winner, the outcome was coded as a 1, whereas if the focal male was a loser, the outcome was coded as a 0. This coding was entered as a binary dependent variable into a generalized linear model with a logit link and binomial errors (Hardy and Field 1998). Independent variables were differences in head length, dewlap size, and bite force between the focal male and the other competitor. Backward stepwise logistic regression was used to determine the "minimum adequate model" (i.e., the simplest model that best describes the data; Crawley 1993; Hardy and Field 1998) for each species (for other examples of minimum adequate models, see Lailvaux et al. 2005; Pomfret and Knell 2006). We used Lillifores tests to assess data normality. Absolute rather than size-adjusted data were compared, as lizards were already size matched for each trial (Lailvaux et al. 2004; Lailvaux and Irschick 2006*b*). However, body size is controlled for in each analysis through the inclusion of head length (an accepted proxy for body size in anoles; Vanhooydonck et al. 2005*a*) as a predictor variable. The use of head length alone is more parsimonious than using both head length and SVL as predictors because inclusion of an additional index of body size in the logistic regressions leads to unacceptable levels of multicollinearity in the data set (tolerances <0.1; Quinn and Keogh 2002). However, as an additional precaution, we also compared SVLs for winners and losers using paired *t*-tests to test for possible body size effects that may confound our results.

Phylogenetic Comparative Analysis. To assess behavioral differences among species during fights, we calculated the proportions of trials in which biting and dewlap display behavior were observed for each species (table 1). We also calculated these proportions for head bobbing because previous studies have shown that bobbing is correlated with locomotor performance in other lizard species (e.g., Brandt 2003). These data were successfully normalized for analysis via arcsin–square root transformations (Sokal and Rohlf 1995). We then calculated and regressed independent contrasts for biting, head bobbing, and dewlapping against contrasts for log sexual size dimorphism (fig. 1; data from Stamps et al. 1997; Butler et al. 2000; regression forced through the origin [Harvey and Pagel 1991]), in order to determine whether the incidences of biting and dewlap display increased with increasing SSD (and hence more intense male-male competition; Stamps et al. 1997). Contrasts were calculated using PDTREE (Garland et al. 1999; Garland and Ives 2000). The phylogeny (fig. 1) and branch lengths used were based on an *Anolis* consensus tree of mitochondrial and genomic DNA constructed using parsimony and Bayesian methods (Nicholson et al. 2005). All statistical analyses were conducted using R and SPSS, version 13.

Results

Honest Signaling

The regression of absolute bite force versus absolute dewlap size was significant for *Anolis sagrei* ($R = 0.333$, $F = 5.477$, df $= 1, 44$, $P = .024$), *A. cristatellus* ($R = 0.785$, $F = 67.61$, df $= 1, 42$, $P < .001$), *A. evermanni* ($R = 0.675$, $F = 40.28$, df $= 1, 48$, $P < .001$), and *A. gundlachi* ($R = 0.756$, $F = 64.09$, df $= 1, 48$, $P < .001$) and tended toward significance in *A. distichus* ($R = 0.274$, $F = 3.399$, df $= 1, 42$, $P < .072$). However, the relationship between dewlap size and bite force was clearly nonsignificant in *A. angusticeps* ($R = 0.114$, $F = 0.848$, df $= 1, 39$, $P < .469$). After correction for body size, significant relationships exist between residual dewlap size and residual bite force in *A. cristatellus*, *A. evermanni*, and *A. gundlachi* but, surprisingly, not in *A. sagrei* (for exact statistics, see legend for fig. 2). *Anolis angusticeps* and *A. distichus* also lacked a significant relationship between size-corrected dewlap size and bite force (fig. 2).

Combat Trials

Bite force and dewlap size showed different patterns for predicting winners and losers within each species. Of the five variables tested, the logistic regression models retained bite force as the only significant predictor of combat suc-

Table 1: Proportion of trials in which dewlap extensions, head bobbing, and biting were observed and log sexual size dimorphism (SSD) values for each *Anolis* species studied

Species	No. individuals	No. trials	Dewlap extensions	Biting	Bobbing	Log SSD
A. angusticeps	42	20	.75	.05	1.00	.14
A. distichus	44	22	.91	.23	.91	.14
A. valencienni	40	17	.65	0	.24	.15
A. carolinensis	48	19	.79	.21	.79	.2
A. sagrei	48	24	.92	.63	1.00	.29
A. evermanni	50	24	.83	.42	.67	.3
A. gundlachi	51	18	.17	.28	.17	.36
A. lineatopus	46	21	.48	.29	.67	.39
A. cristatellus	44	22	.41	.73	.64	.4

Sources: Data on log SSD values are from Stamps et al. (1997) and Butler et al. (2000).

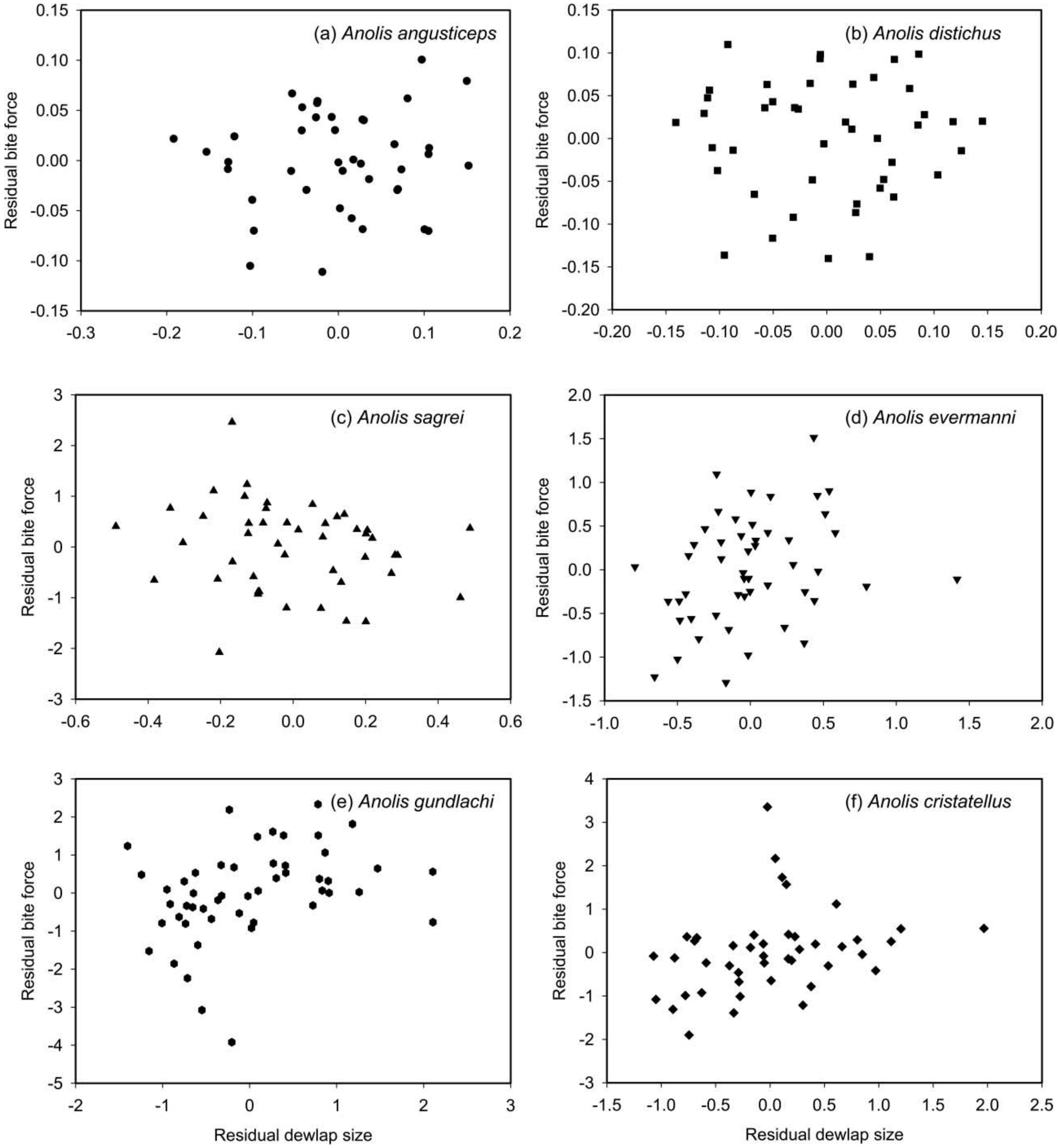

Figure 2: Residual bite force (N) versus residual dewlap size (cm^2) for six *Anolis* species. Residual bite force and residual dewlap size are not correlated in (*a*) *A. angusticeps* ($R = 0.099$, $F = 0.39$, df $= 1, 39$, $P < .536$), (*b*) *A. distichus* ($R = 0.029$, $F = 0.034$, df $= 1, 42$, $P < .854$), or (*c*) *A. sagrei* ($R = 0.18$, $F = 1.47$, df $= 1, 44$, $P < .232$). Residual bite force and residual dewlap size are correlated in (*d*) *A. evermanni* ($R = 0.288$, $F = 4.342$, df $= 1, 48$, $P = .043$), (*e*) *A. gundlachi* ($R = 0.337$, $F = 6.135$, df $= 1, 48$, $P = .017$), and (*f*) *A. cristatellus* ($R = 0.303$, $F = 4.245$, df $= 1, 42$, $P = .046$).

Table 2: Minimum adequate models describing significant predictors of combat outcomes for each *Anolis* species

Species	Variable	Estimated coefficient	SE	df	Change in log likelihood when removed	*P*	Percentage classified correctly
A. angusticeps	Dewlap	2.69	1.49	1	4.12	.042	60
A. distichus	Dewlap	6.64	3.29	1	6.04	.014	72.7
A. valencienni	Dewlap	1.57	.88	1	5.73	.017	70.6
A. carolinensis	Bite	.62	.35	1	5.71	.017	73.7
A. sagrei	Bite	.97	.97	1	5.12	.024	66.7
A. evermanni	Bite	1.71	.94	1	4.6	.032	66.7
A. gundlachi	Bite	.73	.40	1	4.93	.026	66.7
A. lineatopus	Bite	1.75	.75	1	7.9	.005	76.2
A. cristatellus	Bite	1.16	.73	1	3.98	.046	59.1

Note: Models were obtained by separate backward stepwise logistic regression for each species. Change in log likelihood used to determine statistical significance (*P* values) represents the change in model likelihood following removal of the variable in question.

cess in *A. carolinensis*, *A. sagrei*, *A. evermanni*, *A. gundlachi*, *A. lineatopus*, and *A. cristatellus* and dewlap size as the only significant predictor variable in *A. angusticeps*, *A. distichus*, and *A. valencienni* (table 2). Forward and backward stepwise models returned similar results for each species, suggesting that our findings are robust to any perceived problems with stepwise regression analyses (Wittingham et al. 2006). Winners and losers also did not differ significantly in body size (SVL) for any of the nine species studied (see table 3), lending support to the notion that size matching was effective in all cases and that body size has no effect on combat outcomes. These results suggest that bite force and dewlap size differ in their relative importance to male combat in different species depending on level of SSD and, likely, intensity of male combat (fig. 3).

Phylogenetic Comparative Analysis

The regression of contrasts for bite frequency against contrasts for log SSD was significant ($R = 0.71$, $F = 7.116$, $\mathrm{df} = 1, 7$, $P = .032$; fig. 4*a*). In contrast, no significant relationships exist between contrasts for either dewlap extension and log SSD ($R = 0.542$, $F = 2.905$, $\mathrm{df} = 1, 7$, $P < .132$; fig. 4*b*) or head bobbing ($R = 0.095$, $F = 0.064$, $\mathrm{df} = 1, 7$, $P < .808$; fig. 4*c*). Thus, biting appears to occur more frequently in more dimorphic species experiencing more frequent and intense male-male competition than in less dimorphic species (fig. 1).

Discussion

We tested several predictions regarding the relative influence of sexual signal size and bite performance for resolving male fights within each of nine behaviorally divergent anole species. Our results confirm three (1, 2, and, partially, 4, below) of four a priori predictions. Specifically, we found that (1) sexual signal size (dewlap size) was generally an honest signal of bite force in territorial (higher-SSD) but not less territorial (lower-SSD) species, with the exception of one highly dimorphic territorial anole (*A. sagrei*); (2) maximum bite force consistently predicted male combat success in higher-SSD but not lower-SSD species; (3) diametrically opposed to a priori predictions, dewlap size significantly predicted male combat success in lower-SSD but not higher-SSD species; and (4) the incidence of biting but not dewlapping increases as species become more dimorphic (higher SSD). Because of prior work showing strong links between degree of dimorphism and territoriality, this last finding supports the view that more territorial species escalate to biting during fights more readily than less territorial species.

Behavioral Implications

Classic models have detailed how animals resolve fights through a series of escalating stages, although prior authors

Table 3: Results of paired *t*-tests comparing differences in snout-vent length between winners and losers for each *Anolis* species

Species	Mean win (mm)	Mean lose (mm)	*t*	df	*P*
A. angusticeps	50.93	50.58	.94	20	<.361
A. distichus	48.6	49.02	−1.04	21	<.312
A. valencienni	61.80	60.99	1.22	16	<.242
A. carolinensis	66.30	66.02	1.34	18	<.196
A. sagrei	54.73	52.37	1.03	23	<.315
A. evermanni	62.02	61.44	1.71	23	<.101
A. gundlachi	63.48	63.62	−.54	17	<.596
A. lineatopus	54.28	54.21	.23	20	<.818
A. cristatellus	64.80	64.87	−.27	21	<.787

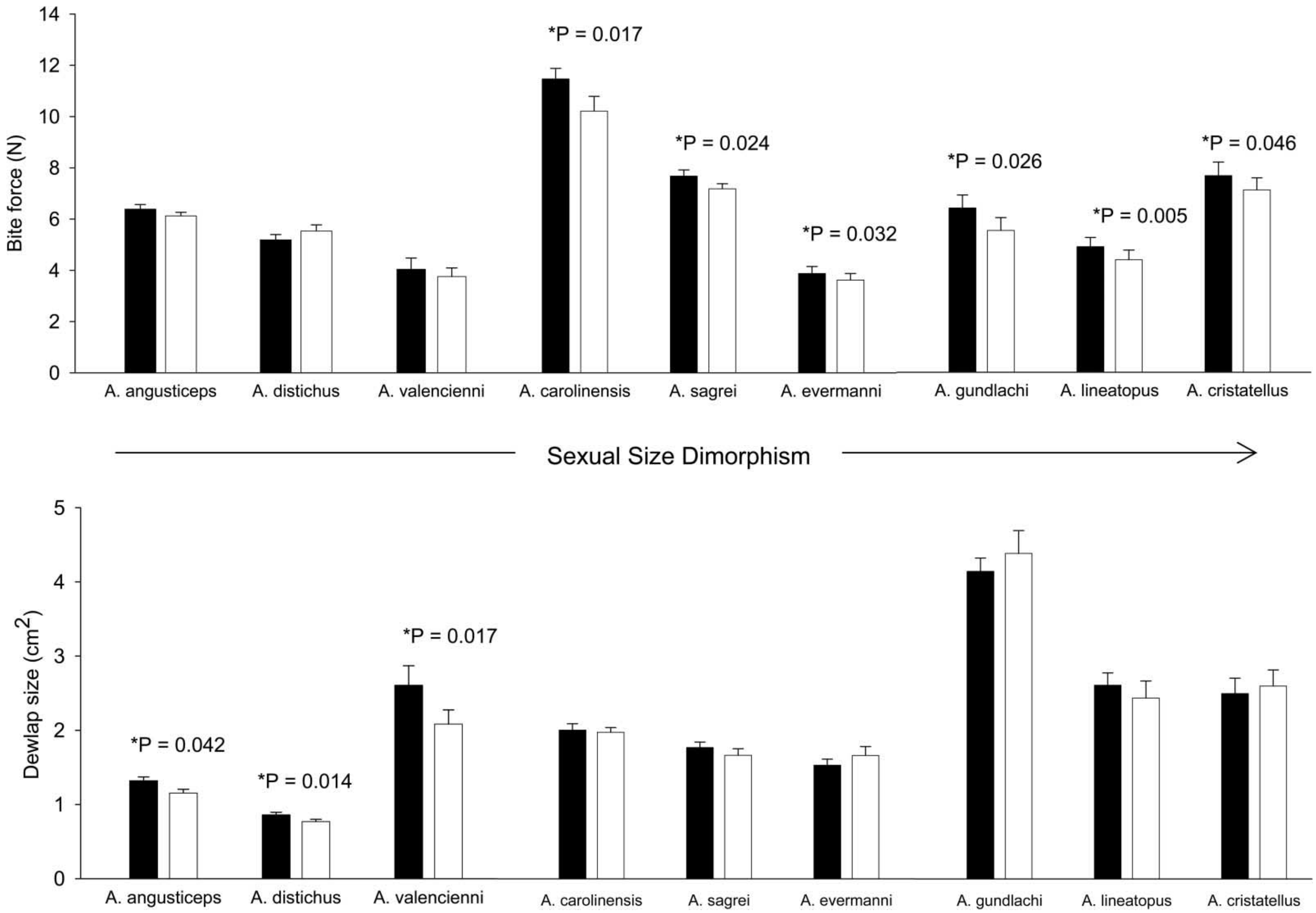

Figure 3: Mean values for dewlap area and maximum bite force in winners (*filled bars*) and losers (*open bars*) for nine species of Caribbean *Anolis* lizards in order of ascending sexual size dimorphism. Bite force, but not dewlap size, was a significant predictor of contest victory in winners in higher–sexual size dimorphism (SSD) species, while dewlap size was the only significant predictor of victory in lower-SSD species. *P* values shown are from multiple logistic regressions and refer to the significance of that particular trait within the model for each species. Error bars represent 1 SE.

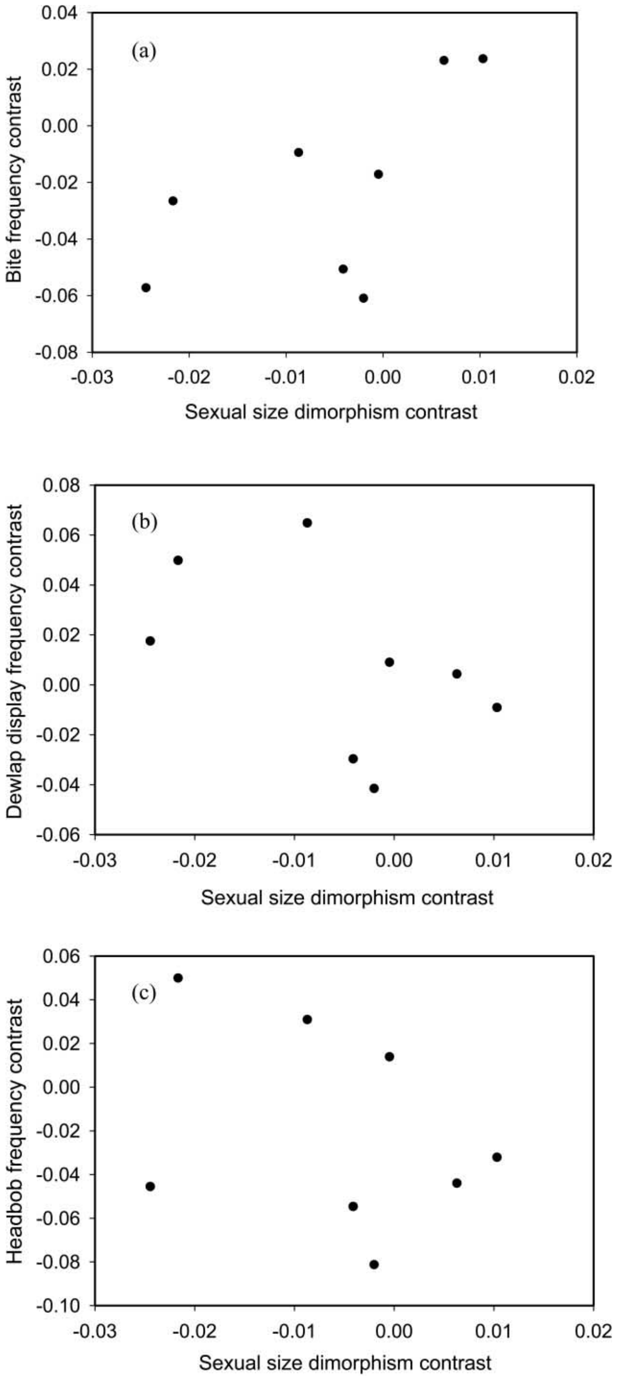

Figure 4: Independent contrasts of log sexual size dimorphism (SSD) versus contrasts of (*a*) arcsin-transformed proportion of trials in which biting was observed ($P = .032$), (*b*) arcsin-transformed proportion of trials in which dewlap extensions were observed ($P < .13$), and (*c*) arcsin-transformed proportions of trials in which head bobs were observed ($P < .808$).

have noted that not every species, and not even all individuals within highly aggressive species, proceed through all stages (Maynard Smith and Harper 2003; Hurd 2006). However, although sexual selection researchers may appreciate this principle in theory, the literature lacks compeling examples of different predictors of contest outcomes as experimentally ascertained by male competition trials across closely related species. Our data set fills this void by showing how species that differ in their intensity of male competition also differ in how they resolve fights. Whereas other studies have examined factors that dictate male competition success (e.g., sexual signal size, performance, male condition; for reviews, see Andersson 1994; Lailvaux and Irschick 2006*a*) within single species, our study makes a large leap forward by expanding this paradigm to nine highly divergent anole species. Our data provide evidence that for less dimorphic and generally less aggressive anole species, conflicts are strongly influenced by the use of sexual signals. This assertion is backed by two lines of evidence. First, there was a relatively strong yet nonsignificant negative evolutionary relationship (Pearson $r = -0.54$) between SSD and the use of dewlapping during male fights. Therefore, less territorial species show a general, though nonsignificant, tendency to use their dewlaps more often during male conflicts compared with territorial species. Second, we found strong evidence that the relative size of the dewlap was a significant predictor of male combat success in lower-SSD anoles. The use of biting during fights was rarely observed in lower-SSD dimorphic anoles (fig. 4), confirming the view that these species resolve fights through nonviolent means. By comparison, territorial, higher-SSD anole species tended to bite each other regularly during male fights (fig. 4), and the most powerful biters tended to win conflicts (table 3; fig. 3).

The view that sexual signals should be "honest" in transmitting accurate information about the internal state of the signaler has received a fair amount of support in the literature (Zahavi 1975; see reviews in Andersson 1994; Lailvaux and Irschick 2006*b*). Although not completely understood for most animal taxa, one obvious function of honest signals is to prevent potentially damaging fights, particularly for lesser-RHP opponents, who are most at risk (Maynard Smith and Harper 2003). Our data are largely consistent with the theory of honest signaling because the relative size of the dewlap was an honest signal of relative bite force for all of the dimorphic, territorial anoles sampled (the lone exception was the territorial anole *A. sagrei*). However, our data also partially contradict this theory because relative dewlap size predicted combat success in less territorial but not territorial anoles. This trend is surprising, given the body of literature showing differences in secondary sexual trait characteristics between winners and losers in several animal taxa (reviewed in Whiting et al. 2003). We suggest that two factors may explain this result, namely, the context in which sexual signals are used and the size-matched nature of our male fights.

There is ample evidence that animals modulate their use of signals according to social context (Maynard Smith and Harper 2003). Extensive behavioral work with anoles shows that males will display their dewlap in both directed (i.e., toward another male) and nondirected (i.e., general territorial behavior) contexts (e.g., Jenssen et al. 2000, 2001), but we know little about whether the information content of the dewlap is transmitted in the same way in the two contexts. We suggest that, for high-SSD, territorial anoles, the dewlap as an honest signal might be relevant for nondirected territorial displays but not during actual male fights. Territorial anoles invest significantly more time in nondirected displays (including large numbers of dewlap displays) for general territorial defense compared with less territorial anoles (Irschick and Losos 1996). We suggest that it is during these nondirected displays that the information content of the dewlap is most relevant for territorial anoles and may play an important role in excluding potential rivals. By comparison, when lizards are placed directly into the most stressful and direct stages of a conflict, due to the close proximity of combatants, functional capacities assume a greater precedence. In the case of higher-SSD anoles, we believe that this close proximity escalated their conflict past the assessment stage and into the final, most violent stage, in which functional capacities are most important. One way of testing this hypothesis would be to investigate patterns of dewlap use and effectiveness at excluding rivals as a function of relative dewlap size and bite force in territorial anoles in the field. On a cautionary note, recent work by Tokarz et al. (2003) casts doubt on the role of the dewlap during general territorial defense in a territorial anole (*A. sagrei*), as they found that males with surgically impaired dewlaps could still defend territories. However, that study, although valuable, was conducted on adult males that already had established territories, and hence removal of their dewlaps may not have affected their dominance status as much as removal of dewlaps in younger males without established territories.

As an additional and potentially interacting factor, the size-matched nature of the male bouts may also promote escalated conflicts. In a field study of the social behavior of *A. lineatopus*, Rand (1967) reported that large males won 85% of observed male-male disputes and that fights became more likely to escalate and the outcomes harder to predict as the difference in body size between combatants decreased. Similarly, Molina-Borja et al. (1998) found that biting in contests between male *Gallotia galloti* lizards occurs only when fighting ability cannot be assessed using "cheaper" behavior (i.e., when the size difference between combatants is small). These results agree with other literature showing that escalated fighting (as opposed to merely ritualized assessment) is especially likely between individuals of similar body sizes in other animal taxa (e.g., Panhuis and Wilkinson 1999; but see Taylor and Elwood 2003). Combat trials in more spacious arenas would be interesting for testing both of the above ideas. Overall, we argue that our results make an important contribution because they challenge the view that honest signals play a key role during intense and directed territorial conflicts in animals, especially among males of similar sizes.

Whereas dewlap size was not important for male combat in the more dimorphic anole species, we found the opposite for lower-SSD anoles: males with relatively larger dewlaps are more likely to win contests. The importance of dewlap size to male fights in lower-SSD anoles is puzzling but is possibly related to the cryptic nature of the more monomorphic ecomorphs examined here. *Anolis valencienni* and *A. angusticeps* lizards are highly cryptic (Hicks and Trivers 1983; Irschick and Losos 1996); they inhabit dense bushes and trees and possess large dewlaps that are displayed only infrequently and typically only to conspecifics that may be relatively far away. Similarly, *A. distichus*, although occurring on broad tree trunks, also possesses cryptic coloration and performs dewlap displays only during agonistic encounters (Jenssen 1983). By contrast, high-SSD, territorial anoles, such as *A. lineatopus*, display their conspicuous bright yellow dewlaps about five times as much as *A. valencienni* (Losos 1990; Irschick and Losos 1996) and in nondirected displays (Rand 1967). Therefore, for cryptic, less dimorphic species that rarely encounter one another in close quarters (Stamps et al. 1997), relatively larger dewlaps may be an effective and startling threat, albeit one that may provide no information on intrinsic male RHP. However, we cannot dismiss the possibility that relative dewlap size in lower-SSD species may be an honest indicator of other aspects of RHP that could be important for conflict resolution or that less dimorphic species may rely on other performance capacities to win fights (Lailvaux and Irschick 2006*a*). Brandt (2003) showed that locomotor endurance capacity is linked to head bobbing in the lizard *Uta stansburiana*; however, we found no significant relationship between the frequency of head bobbing and log SSD across the nine *Anolis* species studied here (fig. 4*c*). Hence, head bobbing is observed just as often during male fights in low- and high-SSD species and is apparently equally important for fights in all species studied. Direct data on other potential performance predictors of fight outcomes in anoles, including locomotor endurance, may shed further light on dewlap use in lower-SSD species.

Evolutionary Implications

Recent syntheses have stressed that sexual selection in general and male competition in particular appear to be key causal factors promoting evolutionary diversification (Schluter 2000; see also Seehausen and Schluter 2004). Our data bear on this point directly by showing that species that differ in ecology, behavior, and SSD also differ in the usefulness of secondary sexual signal size and performance capacities for winning fights. Additionally, unrelated species exhibiting similar behavioral syndromes appear to have converged on similar predictors of fight outcomes. The Caribbean anole radiation represents a classic example of an adaptive radiation that appears to be linked to a sexually selected character (Losos and Chu 1998; Losos et al. 1998). Dewlap size and color in males differ dramatically among males of different anole species (Losos and Chu 1998), but the underlying reasons for this diversity remain poorly understood (Fleishman 1992; Nicholson et al. 2007). One of the primary reasons that the anole dewlap has eluded simple explanation is that one observes enlarged dewlaps in males of both dimorphic, territorial species (e.g., *A. sagrei*) and less dimorphic, less territorial species (e.g., *A. valencienni*). Hence, simple measures of dewlap size alone show only weak correlations with other aspects of anole ecology, behavior, and morphology (Losos and Chu 1998; Nicholson et al. 2007). Our study illuminates part of this mystery by showing that the dewlap itself appears to play different functions in territorial and less territorial species, particularly in how it is used during male fights. In less territorial anoles, dewlaps appear to play an important communication role in directed agonistic displays, and field data indicate that dewlap displays are also important for male-female interactions in such species, which is consistent with the relatively large dewlaps of female anoles of less territorial anole species. By contrast, although the dewlap in territorial anoles may play a key role in establishing dominance hierarchies via nondirected displays (yet unproven), our data indicate that it appears to have little functional significance for directed displays during male fights. In short, the relative size of the dewlap in the anole radiation may be under different selective forces (i.e., nondirected displays in territorial anoles, directed displays in less territorial anoles), and this may explain, in part, why no single ecological or behavioral factor is of overarching importance. We suggest that rather than purely focusing on the size of the male dewlap, examining links between dimorphism in dewlap size and habitat use and behavior may be more fruitful (see also Nicholson et al. 2007). The apparently complex nature of the anole dewlap is likely typical of many sexual signals that are used for multiple purposes (e.g., used in male-male, male-female, and predator-prey encounters), reinforcing the need for an integrative approach.

Conclusions

In conclusion, our analysis of male combat reveals two predictors of fight outcomes among nine divergent anole species: one based on performance (territorial, high-SSD species) and the other based on dewlap size and signaling (less territorial, lower-SSD species). These findings have profound implications for behavioral studies because they suggest that the ecological and behavioral qualities of species may modify not only the shape and size of sexually selected traits (Fleishman 1992; Endler and Basolo 1998) but also the nature of the information those traits convey. Indeed, our data indicate that the role of the *Anolis* dewlap as an index of RHP may be overly simplistic (see also Losos and Chu 1998; Tokarz et al. 2003). Another noteworthy result is convergence in conflict resolution among the same ecomorphs that have independently evolved on different islands, lending support to the general view that species sharing similar ecological characteristics will exhibit similar behavioral syndromes as well.

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