



INVITED PERSPECTIVES

Intraspecific Variation in the Information Content of an Ornament: Why Relative Dewlap Size Signals Bite Force in Some, But Not All Island Populations of *Anolis sagrei*

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Synopsis In many animals, male secondary sexual traits advertise reliable information on fighting capacity in a male–male context. The iconic sexual signaling device of anole lizards, the dewlap, has been extensively studied in this respect. For several territorial anole species (experiencing strong intrasexual selection), there is evidence for a positive association between dewlap size and bite capacity, which is an important determinant of combat outcome in lizards. Intriguingly, earlier studies did not find this expected correlation (relative dewlap size–relative bite force) in the highly territorial brown anole lizard, *Anolis sagrei*. We hypothesize that the dewlap size–bite force relationship can differ among populations of the same species due to interpopulation variation in the degree of male–male competition. In line with this thought, we expect dewlap size to serve as a reliable predictor of bite performance only in those populations where the level of intrasexual selection is high. To tackle this hypothesis, we examined the relationship between male dewlap size and bite force on the intraspecific level in *A. sagrei*, using an extensive dataset encompassing information from 17 island populations distributed throughout the Caribbean. First, we assessed and compared the relationship between both variables in the 17 populations under study. Second, we linked the relative dewlap size–bite force relationship within each population to variation in the degree of intrasexual selection among populations, using sexual size dimorphism and dewlap display intensity as surrogate measures. Our results showed that absolute dewlap size is an excellent predictor of maximum bite force in nearly all *A. sagrei* populations. However, relative dewlap size is only an honest signal of bite performance in 4 out of the 17 populations. Surprisingly, the level of signal honesty did not correlate with the strength of intrasexual selection. We offer a number of conceptual and methodological explanations for this unexpected finding.

Introduction

The evolution of male secondary sexual traits, such as the colossal antlers in deer or the giant horns in rhinoceros beetles, has fascinated biologists ever since Darwin (1871; Andersson 1982; Bradbury and Vehrencamp 1998; Emlen 2008). These elaborate sexual traits can function as real weapons to overpower or even kill male opponents (e.g., mandibles of male fig wasps; Bean and Cook 2001), but also as reliable signals advertising “fighting capacity” without playing a role during actual physical combats (e.g., red coloration in male mandrills; Setchell and Wickings

2005). Traits that honestly signal fighting capacity seem highly beneficial to predict contest outcomes and thereby avoid the costly interactions physical combats may impose (Andersson 1994). This is especially true for species where actual fights between males can result in serious body damage and even in death (e.g., wasps, Bean and Cook 2001; Abe et al. 2003; spiders, Leimar et al. 1991). The idea that male secondary sexual signals communicate reliable information about quality in an intrasexual context has been evidenced by a variety of studies showing a direct link between variation in signal design

(especially size and color) and the ability to win male contests (e.g., Jennions and Backwell 1996; Panhuis and Wilkinson 1999; Alonso-Alvarez et al. 2004). In many cases, the size of these sexual traits correlates strongly with overall body size (arguably the most important predictor of contest outcome (e.g., Clutton-Brock et al. 1979; Hughes 1996; Karsten et al. 2009; Hardy and Briffa 2013), and as such acts as a redundant or back-up signal (Zuk et al. 1992; Johnstone 1996; Candolin 2003) when advertising fighting capacity. However, in at least some cases, the size of secondary sexual traits reveals more than just the carrier's overall body size during agonistic interactions. Here, sexual signal size contains information on fighting capacity independent of overall body size (i.e., relative size), and can therefore be considered as a reliable signal in itself. In dung beetles, for example, relative male horn size accurately predicts pulling force and maximal exertion, two ecologically relevant performance measures associated with fighting success in beetles (Lailvaux et al. 2005). Also in lizards, male signals can act as size-free indices of fighting capacity, quantified by endurance or bite force (e.g., Perry et al. 2004; Lappin and Husak 2005; Vanhooydonck et al. 2005a). Anole lizards in particular have received considerable attention in this respect (e.g., Lailvaux et al. 2004; Vanhooydonck et al. 2005b; Lailvaux and Irschick 2007). They typically have an extendible throat fan, called a dewlap. This sexually selected trait is generally far more elaborated in the male sex and is exceptional for its high degree of interspecific variation in design (Nicholson et al. 2007; Johnson and Wade 2010). Besides, anoles exhibit varying degrees of territoriality and male–male competition (Losos 2009; Johnson et al. 2009; Kamath and Losos 2017), also reflected by their remarkable diversity in sexual size dimorphism (SSD; i.e., predominantly male-biased SSD) (Stamps et al. 1997; Ord et al. 2001; Butler et al. 2007).

One obvious question that arises is whether dewlap size indicates fighting capacity in *Anolis* lizards? The evidence is rather mixed. In highly territorial, sexually dimorphic (high-SSD) species (i.e., *A. carolinensis*, *A. cristatellus*, *A. evermanni*, *A. gundlachi*, and *A. lineatopus*), relative dewlap size predicts bite force and thus seems to contain detailed information on fighting capacity (Vanhooydonck et al. 2005a; Lailvaux and Irschick 2007). However, no such relationship was found in less dimorphic (low-SSD) species (i.e., *A. angusticeps*, *A. distichus*, and *A. valencienni*; Vanhooydonck et al. 2005a; Lailvaux and Irschick 2007). The authors explain the lack of this relation in less dimorphic species preliminary by

a low degree of territoriality. Bite performance, in particular, might be far less important for males of species that do not actively defend territories or that do not experience a high degree of male–male competition associated with vigorous fights. Lailvaux and Irschick (2007) further corroborated this idea by showing that bite force predicted male combat success only in the high-SSD species and that the incidence of biting increased with SSD.

Intriguingly, one species in their dataset defied this putative principle: *Anolis sagrei*, albeit clearly sexually dimorphic, did not show the expected positive correlation between relative dewlap size and bite performance (although a significant relationship was found between absolute dewlap size and bite force). In accordance, Driessens et al. (2015) also failed to find such a relationship in wild-caught males from Florida, when looking at relative indices. Because of these unexpected results, we aimed to further explore the dewlap size–bite force relationship in this polygynous and highly territorial species (Schoener and Schoener 1980; Tokarz 1998, 2002). Direct physical combats are commonly observed among brown anole males and primarily involve biting, jaw sparring, and interlocking (Scott 1984; Tokarz 1985, 1987; McMann 2000; Steffen and Guyer 2014; Driessens et al. 2014). *Anolis sagrei* has a yellow-to-reddish dewlap that can show dramatic intraspecific variation in size, color, pattern, and even use (Vanhooydonck et al. 2009; Edwards and Lailvaux 2012; Driessens et al. 2017). Adult males primarily use dewlap displays in combination with push-ups and head-bobs for territorial defense and/or for access to females (e.g., Scott 1984; Simon 2011; Driessens et al. 2014). Recently, display behavior and dewlap color have been reported to predict the outcome of staged contests between size-matched males (Steffen and Guyer 2014), further demonstrating the role of the *A. sagrei* dewlap in signaling quality to opponents (but see Tokarz et al. 2003). Close-proximity contest experiments additionally revealed that *A. sagrei* males with enhanced biting capacities are at a competitive advantage for winning fights (Lailvaux and Irschick 2007), highlighting the importance of signaling bite capacity too, during agonistic interactions.

The main goal of this study is to look in more detail at the relationship between male dewlap size and bite force, explicitly for *A. sagrei*. Therefore, we took an intraspecific comparative approach, documenting and comparing this specific relationship in 17 *A. sagrei* island populations distributed across the Caribbean. We looked at the relationship between dewlap size and bite force, using absolute as well

as relative indices. Consistent with previous studies, we expected absolute dewlap size to be a good predictor of absolute bite force for each study population (Lailvaux and Irschick 2007; Cox et al. 2009; Driessens et al. 2015). However, we hypothesize that the relative dewlap size–bite force relationship will differ among populations due to interpopulation variation in the degree of male–male competition. In line with this thought, we expect dewlap size to serve as a reliable predictor of bite performance only in those populations where the level of intrasexual selection is high (following Lailvaux and Irschick 2007). To do so, we linked the dewlap size–bite force relationship within each population to both SSD and display intensity (DI) among populations, taking into account phylogenetic relationships.

Materials and methods

Animals

We sampled a total of 639 adult *A. sagrei* males from 17 populations distributed across the Caribbean (Fig. 1). Sampling localities included Acklins, Andros, Chub Cay, Crooked Island, Grand Bahama, Pidgeon Cay, Staniel Cay (data collection for these seven populations occurred in April–May 2003), Jamaica (March 2012), Cuba (Santa Clara, Soroa 1, Soroa 2; April–May 2012), San Salvador (January 2013), Cayman Islands (Cayman Brac, Grand Cayman, Little Cayman; March 2013), South Abaco, and South Bimini (March 2015). Since previous studies on *A. carolinensis* have reported a significant effect of seasonality on dewlap size, bite force, and display behavior (Jenssen et al. 1995, 2001; Irschick et al. 2006; Lailvaux et al. 2015), data were collected during the *A. sagrei* breeding season (March–September, Lee et al. 1989), apart from one population (i.e., San Salvador) that was sampled in January. We caught 404 *A. sagrei* males by noose and kept them individually in plastic bags for maximum 48 h, before releasing them back at the location of capture. For these individuals, we measured morphology, quantified dewlap size, and carried out standard bite force measurements. Another 235 male individuals (but only for ten populations) were video-recorded while behaving in their natural habitat.

Morphology

We measured the lizards' snout–vent length (SVL) and head length (HL; from the tip of the snout to the posterior edge of the parietal scale) using digital calipers (Mitutoyo CD-15DC, accuracy 0.01 mm). For measuring dewlap size, lizards were first positioned on their left side against a 1-cm² gridded paper. We then gently pulled the base of the ceratobranchial forward

with a pair of forceps until the dewlap was fully extended parallel to the grid (Bels 1990). Next, we photographed the dewlap, using a Nikon D70 camera mounted on a tripod. Last, Adobe Photoshop CS3 extended software (AP CS3, version 10.0) was used to trace the outer edge of the dewlap on the digital images and to calculate absolute dewlap area. This standard method for measuring dewlap dimensions has produced highly repeatable results in a previous study (Vanhooydonck et al. 2005a).

Bite force

Standard methods were used to measure maximum bite force. Briefly, we encouraged lizards to bite on two metal plates connected to an isometric Kistler force transducer (type 9203) and charge amplifier (type 5995); for detailed descriptions of setup and biting procedure, see Herrel et al. (1999a) and Vanhooydonck et al. (2005b). Each individual was subjected to a total of five bite trials with approximately 30 min in between (as in e.g., Herrel et al. 2001; Lailvaux et al. 2004; Irschick et al. 2006; Lailvaux and Irschick 2007). The highest of the five bite force measurements was then used as the maximal bite force capacity in each individual. The applied methodology has been widely used and shown to be effective for obtaining maximal bite forces in lizards (e.g., Herrel et al. 2001; Lailvaux et al. 2004; Vanhooydonck et al. 2005b; Lailvaux and Irschick 2007; Baeckens et al. 2017). Since temperature is known to affect bite performance (Bennett 1985; Herrel et al. 1999b; Anderson et al. 2008), we made sure every lizard had a body temperature between 29°C and 31°C prior to every bite trial (the average field-active body temperature of *A. sagrei* is 30.6°C; Losos 2009). Body temperature was verified using a cloacal thermometer (APPA51, K-type).

Sexual size dimorphism

Consistent with Lailvaux and Irschick (2007, and references therein), we calculated SSD as mean SVL in males divided by mean SVL in females. Values of SSD were calculated for each population, and only SVLs of mature males and females were included.

Display intensity

As in Driessens et al. (2017), we recorded the natural behavior of 20–30 males per population (ten study populations) for a timespan of 10 min, using a high-definition camera (Sony, HDR-CX260VE). First, we located lizards by walking slowly through their natural habitat until an apparently undisturbed individual was spotted. Next, we started filming the lizard's

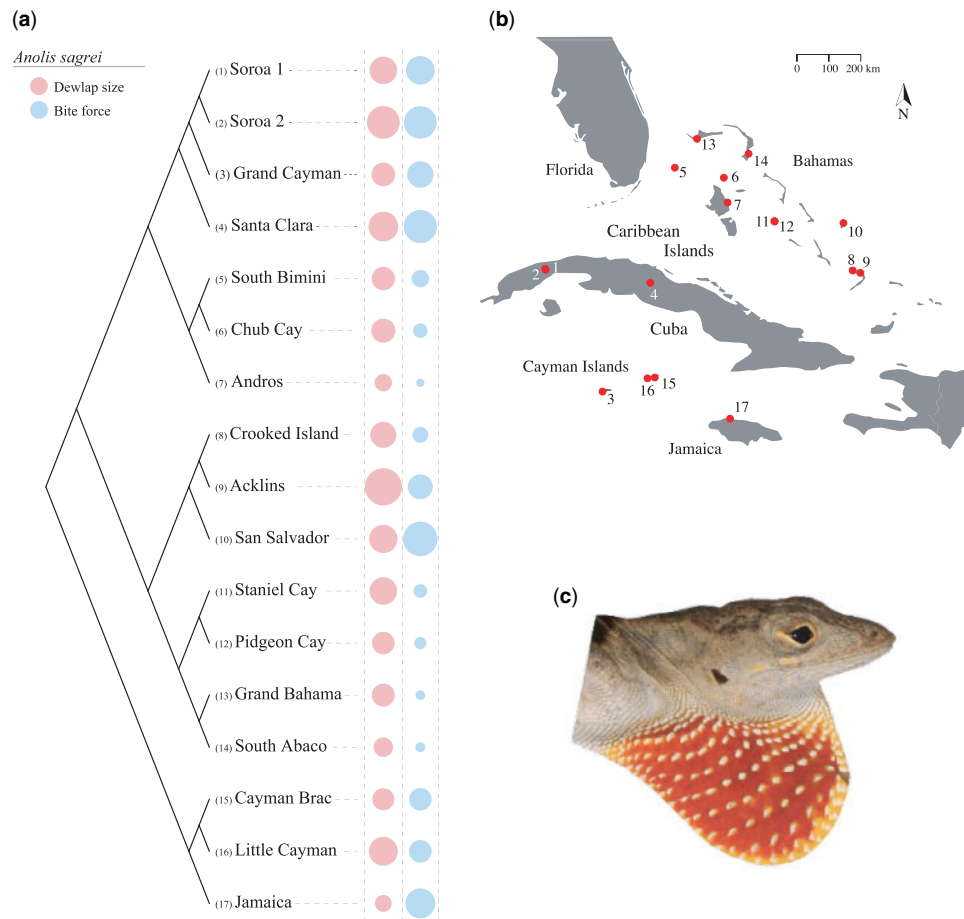


Fig. 1 (a) Phylogenetic relationships among the 17 *Anolis sagrei* study populations presented with corresponding sampling sites (b) distributed across the Caribbean. Circle size represents the mean dewlap size (red) and bite force (blue) of a population. Photograph (c) showing the large dewlap of a male *A. sagrei* lizard.

behavior from approximately 5–15 m using the camera zoom function (30 \times optical zoom), in order to minimize disturbances caused by our presence. Video recordings were only made during sunny or partly cloudy conditions to avoid possible confounding effects of weather on the lizard's activity level (Huey 1982; Hertz et al. 1993). All behavioral recordings were scored offline, using JWatcher event-recorder software (Blumstein and Daniel 2007). For each focal individual, we noted the number and duration of three main display types: head-nods (up-and-down movement of the head), push-ups (up-and-down movement of the body and tail caused by flexion of the legs), and dewlap extensions (pulsing of the dewlap). These displays can function in species recognition (e.g., Rand and Williams 1970; Losos 1985), in predator deterrence (e.g., Leal and Rodríguez-Robles 1995, 1997), but most often in social and sexual communication (e.g., Greenberg and Noble 1944; Jenssen 1970; Crews 1975; Carpenter 1978; Driessens et al. 2014; Baeckens et al. 2016). Moreover, DI is typically inter-correlated in

the sense that males that frequently perform one display type also exhibit the other types at a high rate (e.g., Scott 1984; McMann 2000; Driessens et al. 2014; Steffen and Guyer 2014). In the remaining, “DI” refers to the proportion of time that individuals spent displaying in their natural setting during the 10 min observation period (averaged per population).

Statistical analyses

Prior to statistical analyses, data on HL, dewlap size, bite force, and SSD were log₁₀-transformed. Proportion data (i.e., DI) were normalized via arcsin-square root transformation (Sokal and Rohlf 1995). In all cases, assumptions of normality were confirmed using Shapiro–Wilk tests, and probabilities (*P*) lower than 0.05 were considered significant.

All statistical tests involving dewlap size and bite force were done with absolute as well as relative (i.e., size-corrected) data. Consistent with Vanhooydonck et al. (2005a) and Lailvaux and Irschick (2007), we

used HL for removing effects of overall size. This metric strongly correlated with dewlap size and bite force, and has previously proven to be most appropriate for calculating relative indices of these two variables (Vanhooydonck et al. 2005a; Herrel and O'Reilly 2006). Relative bite force and dewlap size were calculated by regressing \log_{10} bite force and \log_{10} dewlap size against \log_{10} HL and, subsequently, by extracting the residual values for all individuals.

We first ran a univariate general linear model (GLM) to test whether the relationship between dewlap size and bite force (independent and dependent variable, respectively) differed among our study populations. HL was then added to the model as a covariate, to assess the same effects after size correction. Both GLM analyses revealed significant dewlap size * population interaction effects on bite force, which impelled us to subsequently examine this relationship separately within populations. We therefore carried out linear regressions per population with dewlap size as independent and bite force as dependent variable. Following Lailvaux and Irschick (2007), we obtained relative indices by regressing dewlap size and bite force against HL and calculating the residuals for all individuals per population. We then ran a second set of linear regressions, this time with relative bite force against relative dewlap size (i.e., residuals; consistent with Vanhooydonck et al. 2005a; Lailvaux and Irschick 2007).

Among-population analyses were performed in an explicit phylogenetic context in order to account for the non-independency of our data points (Felsenstein 1985; Harvey and Pagel 1991). We used the phylogenetic tree proposed by Driessens et al. (2017) in all phylogenetic comparative analyses. Driessens' tree was created using the exact same populations sampled in this study. To test the idea that reliable information content of the dewlap in itself depends on the local intensity of intrasexual selection, we regressed the slope of the relative “dewlap size–bite force” regression line for each population (i.e., coefficient b) against SSD and DI, respectively. We here employed phylogenetic generalized least squares (pgls) regressions with incorporation of phylogenetic relationships on population level (caper package R, Orme et al. [2013]; for a detailed description of the used phylogenetic tree, see Driessens et al. 2017). This method uses maximum likelihood to simultaneously estimate the regression model and phylogenetic signal (Pagel's λ) of the residual error (Garland and Ives 2000; Revell 2010), and has shown to do better than a priori tests of phylogenetic signal;

especially when sample sizes are smaller than 20 (Blomberg et al. 2003; Revell 2010; Kamilar and Cooper 2013). Because data from one population (i.e., San Salvador) could only be collected outside the breeding season, we ran an additional set of the same pgls regression analyses excluding these particular data.

Results

Population means and standard deviations for tested variables are provided in Table 1. The relationship between dewlap size and bite force differed significantly among populations ($F_{16, 381} = 14.93$, $P < 0.0001$), also after correcting for body size ($F_{16, 380} = 9.36$, $P < 0.0001$). Within-population regression analyses revealed that absolute dewlap size is an excellent predictor of absolute bite force in nearly all study populations ($R > 0.65$, $P < 0.005$, Table 2); only for the population of Santa Clara the relationship failed to reach the conventional level of statistical significance ($R = 0.38$, $P = 0.054$). However, after correcting for body size, in only 4 out of the 17 tested populations, relative dewlap size still exhibited a significant positive relationship with bite force (Table 2 and Fig. 2). We additionally observed that these results based on relative indices varied widely across populations with estimated slopes ranging from -0.353 in Little Cayman to $+0.729$ in South Abaco (Table 2). Overall, results of the population sampled outside the breeding season (i.e., San Salvador) did not deviate from the other study populations sampled during the reproductive cycle in *A. sagrei* (both absolute and relative indices, Tables 1 and 2 and Fig. 1).

An among-population regression analysis (pgls) failed to find a significant association between the relative dewlap size–bite force relationship (i.e., slope coefficient b) and SSD ($R = 0.11$, $df = 16$, $P = 0.662$). Thus, in populations characterized by larger SSD, dewlap size in itself was not a more reliable signal of bite force than in populations characterized by lower SSD. The same applies to DI, as no significant correlation was found between the relative dewlap size–bite force relationship and DI ($R = 0.23$, $df = 9$, $P = 0.532$). Excluding the population of San Salvador from the pgls regressions did not alter any of our results (results remained non-significant, SSD: $R = 0.12$, $df = 15$, $P = 0.657$ and DI: $R = 0.13$, $df = 8$, $P = 0.747$).

Discussion

By studying a series of island populations, we here present our findings on the reliability of dewlap

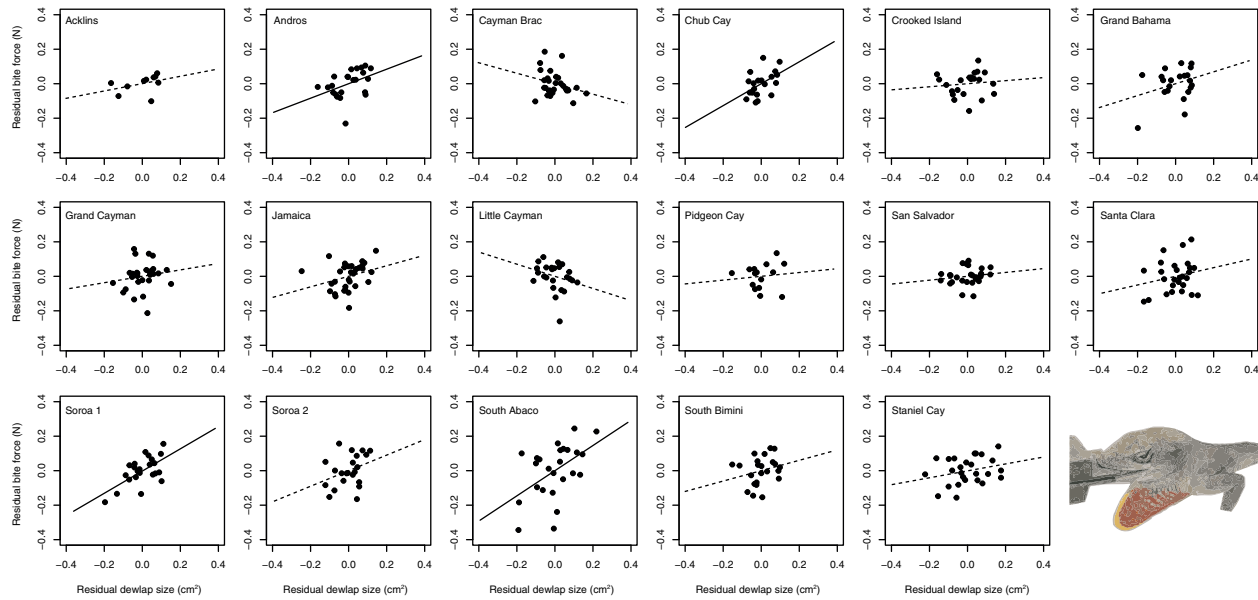


Fig. 2 Relative bite force regressed against relative dewlap size for each *A. sagrei* population, separately. Straight regression lines represent a significant correlation between both variables, i.e., Andros, Chub Cay, Soroa 1, and South Abaco. Dotted regression lines represent no significant relationship between relative dewlap size and bite force. Detailed statistics are provided in Table 2. The illustration (right, below) visualizes a male brown anole biting on a purpose-built force plate.

Table 1 Descriptive statistics of the tested variables

Populations	HL (mm)	SVL (mm)	Dewlap size (cm ²)	Bite force (N)	SSD	DI
Acklins	15.09 ± 1.06 (10)	56.36 ± 5.24 (10)	2.58 ± 0.68 (10)	5.75 ± 1.45 (10)	1.43 (10, 12)	—
Andros	12.81 ± 0.87 (23)	46.37 ± 3.25 (23)	1.21 ± 0.33 (23)	1.90 ± 0.51 (23)	1.23 (23, 18)	—
Cayman Brac	15.19 ± 1.03 (28)	55.07 ± 4.30 (28)	1.53 ± 0.39 (28)	5.22 ± 1.65 (28)	1.33 (28, 29)	0.01 ± 0.03 (23)
Chub Cay	13.92 ± 0.88 (20)	47.87 ± 3.62 (20)	1.67 ± 0.49 (20)	3.36 ± 0.92 (20)	1.32 (20, 16)	—
Crooked Island	13.68 ± 1.04 (23)	49.86 ± 4.61 (23)	1.81 ± 0.61 (23)	3.66 ± 1.34 (23)	1.25 (23, 20)	—
Grand Bahama	12.82 ± 1.43 (24)	46.78 ± 6.34 (24)	1.59 ± 0.41 (21)	2.26 ± 1.39 (24)	1.33 (24, 11)	—
Grand Cayman	14.47 ± 1.21 (27)	51.74 ± 4.57 (27)	1.64 ± 0.41 (27)	6.11 ± 2.19 (27)	1.28 (27, 29)	0.07 ± 0.11 (24)
Jamaica	13.92 ± 1.00 (32)	48.60 ± 3.98 (32)	1.17 ± 0.27 (32)	6.90 ± 2.17 (32)	1.24 (32, 23)	0.02 ± 0.03 (22)
Little Cayman	15.17 ± 1.06 (28)	53.46 ± 4.35 (28)	2.00 ± 0.56 (28)	5.22 ± 1.57 (27)	1.29 (28, 27)	0.01 ± 0.01 (23)
Pidgeon Cay	14.15 ± 0.80 (16)	48.19 ± 3.28 (16)	1.56 ± 0.39 (16)	2.82 ± 0.79 (16)	1.21 (16, 8)	—
San Salvador	16.27 ± 1.52 (27)	58.13 ± 5.85 (27)	1.96 ± 0.75 (27)	7.99 ± 2.24 (27)	1.35 (27, 14)	0.02 ± 0.02 (24)
Santa Clara	15.80 ± 0.82 (27)	55.21 ± 2.97 (27)	2.06 ± 0.36 (27)	7.68 ± 1.78 (27)	1.33 (27, 24)	0.18 ± 0.13 (24)
Soroa 1	14.84 ± 1.35 (23)	51.10 ± 4.44 (23)	1.91 ± 0.45 (23)	6.63 ± 1.94 (23)	1.24 (23, 21)	0.11 ± 0.11 (24)
Soroa 2	15.50 ± 1.03 (22)	55.45 ± 4.46 (22)	2.27 ± 0.46 (22)	7.53 ± 2.00 (22)	1.32 (22, 24)	0.17 ± 0.14 (30)
South Abaco	13.07 ± 1.16 (26)	46.59 ± 4.15 (26)	1.35 ± 0.48 (26)	2.27 ± 0.96 (25)	1.28 (26, 21)	0.02 ± 0.04 (21)
South Bimini	14.91 ± 1.38 (24)	53.66 ± 4.60 (27)	1.62 ± 0.45 (26)	4.04 ± 1.13 (24)	1.30 (27, 23)	0.02 ± 0.02 (20)
Staniel Cay	13.86 ± 1.16 (26)	51.82 ± 5.41 (26)	1.91 ± 0.69 (26)	3.14 ± 1.05 (26)	1.32 (26, 20)	—

Notes: Population means ± standard deviations are presented for each population, with the exception of SSD (i.e., mean SVL males divided by mean SVL females). Sample sizes are provided between brackets for each variable separately; for SSD the number of implemented males and females is shown (left and right, respectively). HL, head length; SVL, snout-to-vent length; SSD, sexual size dimorphism; DI, display intensity, as the proportion of time that individuals spent displaying.

size as a predictor for bite performance in a territorial Caribbean anole, and how this dewlap size–bite force relationship varies so drastically among populations. We used absolute and

relative indices to assess the link between dewlap size and bite force, as both indices can differ in the messages they convey (Lailvaux and Irschick 2007).

Table 2 Univariate linear regression analyses of bite force (dependent variable) against dewlap size (independent variable) within population

Population	R	F	df	Coefficient $b \pm SE$	P-value
Absolute bite force against dewlap size					
Acklins	0.819	16.28	9	0.761 \pm 0.189	0.004
Andros	0.806	38.81	22	0.758 \pm 0.122	<0.001
Cayman Brac	0.652	19.28	27	0.792 \pm 0.180	<0.001
Chub Cay	0.909	85.16	19	0.948 \pm 0.102	<0.001
Crooked Island	0.810	40.09	22	0.828 \pm 0.131	<0.001
Grand Bahama	0.723	20.82	20	1.503 \pm 0.329	<0.001
Grand Cayman	0.784	39.87	26	0.156 \pm 0.183	<0.001
Jamaica	0.740	36.31	31	0.933 \pm 0.155	<0.001
Little Cayman	0.704	23.55	25	0.682 \pm 0.141	<0.001
Pidgeon Cay	0.708	14.03	15	0.622 \pm 0.166	0.002
San Salvador	0.904	112.0	26	0.637 \pm 0.060	<0.001
Santa Clara	0.375	4.093	26	0.471 \pm 0.233	0.054
Soróa 1	0.870	65.69	22	1.078 \pm 0.133	<0.001
Soróa 2	0.795	34.45	21	1.254 \pm 0.214	<0.001
South Abaco	0.762	31.89	24	0.936 \pm 0.166	<0.001
South Bimini	0.729	23.77	22	0.670 \pm 0.137	<0.001
Staniel Cay	0.799	42.48	25	0.651 \pm 0.100	<0.001
Relative bite force against relative dewlap size					
Acklins	0.380	1.352	9	0.214 \pm 0.184	0.278
Andros	0.413	4.328	22	0.420 \pm 0.202	0.050
Cayman Brac	0.266	1.972	27	−0.303 \pm 0.216	0.172
Chub Cay	0.490	5.679	19	0.635 \pm 0.267	0.028
Crooked Island	0.108	0.249	22	0.089 \pm 0.178	0.623
Grand Bahama	0.305	1.955	20	0.345 \pm 0.246	0.178
Grand Cayman	0.153	0.603	26	0.185 \pm 0.239	0.445
Jamaica	0.312	3.230	31	0.306 \pm 0.170	0.082
Little Cayman	0.273	1.937	25	−0.353 \pm 0.254	0.177
Pidgeon Cay	0.221	0.720	15	0.186 \pm 0.219	0.411
San Salvador	0.166	0.707	26	0.112 \pm 0.134	0.411
Santa Clara	0.212	1.177	26	0.251 \pm 0.232	0.288
Soróa 1	0.623	13.36	22	0.639 \pm 0.175	0.001
Soróa 2	0.335	2.523	21	0.451 \pm 0.284	0.128
South Abaco	0.495	7.460	24	0.729 \pm 0.267	0.012
South Bimini	0.243	1.318	22	0.301 \pm 0.262	0.264
Staniel Cay	0.271	1.907	25	0.198 \pm 0.144	0.180

Notes: Results are shown for regressions with absolute and relative variables, respectively. Significant results ($P < 0.05$) are shown in bold font.

Absolute dewlap size–bite force relationship

Our results revealed that dewlap size is an excellent predictor of bite force capacity in nearly all study populations. A strong association between absolute dewlap size and bite force in *A. sagrei* males has also been reported in all previous studies (Lailvaux and Irschick 2007; Cox et al. 2009; Driessens et al. 2015),

emphasizing the generality of this finding. In many animal species, including *A. sagrei*, body size is the key predictor in determining combat outcome, with larger individuals having a substantial advantage over smaller ones (e.g., Tokarz 1985; Hughes 1996; Hardy and Briffa 2013). Gathering accurate information on the opponent's body size (assessment game) seems

thus crucial to avoid costs associated with escalated fights (Andersson 1994; Emlen 2008). Yet, in reality, the accurate transmission of information is often impeded by ambient noise (e.g., precipitation, low light levels, and windblown vegetation), and particularly when only one signal component is involved (e.g., Fleishman 1992; Lengagne and Slater 2002; Peters and Evans 2003; Leonard and Horn 2005). A commonly adopted signaling strategy to cope with such impeding factors is to repeat the same message in different ways by using redundant signal components (e.g., Zuk et al. 1992; Møller and Pomiankowski 1993; Johnstone 1996). Within all our study populations, absolute dewlap size correlated strongly with overall body size and might as such, serve as a redundant signal for body size to increase signal accuracy during mate assessment. Characterized by a brown to grayish body color, *A. sagrei* is well camouflaged in the microhabitats it usually occupies (trunk-ground ecomorph; Schoener and Schoener 1982; Losos 2009). In contrast, its bright yellow to reddish dewlap is highly conspicuous, due to high color and pattern contrasts with background vegetation (Endler 1992, 1993, 2012). Thus, by using the combination of a more cryptic body together with a conspicuous dewlap, males can transmit more accurate information on size and consequently, fighting capacity to opponents. The potential role of the *A. sagrei* dewlap as redundant signal for body size might be most prominent during the early stages of opponent assessment, when signaling still occurs over relatively long distances (more ambient noise), or perhaps during territorial advertisement in order to discourage unseen rival males from intruding (McMann 1998; Orrell and Jenssen 2003). Accordingly, Henningsen and Irschick (2012) showed in their study that surgically reducing the size of the dewlap did not change the outcome of staged close-proximity interactions between size-matched *A. carolinensis* males; bite force capacity in itself appeared to be more important in determining the outcome of these staged interactions. Based on their results, the authors suggested that dewlap size functions as a signal of bite force primarily during non-directed, long-distance territorial displays, whereas more direct means of assessing one another (e.g., jaw size, head size, body condition, push-ups) may be of higher importance during close-proximity aggressive interaction. In this respect, future behavioral experiments on *A. sagrei* testing the importance of absolute dewlap size as a redundant signal for size during long-distance versus short-distance male interactions might be a valuable addition.

Relative dewlap size–bite force relationship

In addition to conveying information on body size, a sexual trait can function as direct, honest signal for advertising fighting capacity (e.g., Panhuis and Wilkinson 1999; Lailvaux et al. 2005). Evidence for a positive link between relative male dewlap size and bite force during the breeding season has been shown for several territorial anole species (Vanhooydonck et al. 2005a; Lailvaux and Irschick 2007). Surprisingly, earlier studies did not observe this correlation in the highly territorial brown anole lizard, *A. sagrei* (Lailvaux and Irschick 2007; Cox et al. 2009; Driessens et al. 2015). By examining a large set of island populations, we now also found support for a significant relationship between relative dewlap size and bite force within *A. sagrei*, though, only in 4 out of the 17 tested populations. In contrast to our expectations, the degree of SSD and DI could not explain the observed variation in the relative dewlap size–bite force relationship found among our populations. Thus, populations where relative dewlap size appeared to be an honest signal of bite force were not *per se* characterized by a higher degree of intrasexual selection, which is inconsistent to earlier findings from Lailvaux and Irschick (2007) (at the species level). Standard errors of the estimated slopes for the relative dewlap size–bite force relationships fell within a relatively narrow range (0.134–0.284, Table 2), and we therefore believe that our failure to find an association between the slopes and SSD or DI is due to the low among-population differences in variance. Another potential reason why we fail to find an association might be due to relative low sample sizes. While the majority of regression analyses showed a high statistical power (power > 0.99), hence, adequate sample sizes, analyses on the populations where relative bite force was not significantly correlated with relative dewlap size were characterized by a relative low statistical power (power < 0.5). Although our sample sizes and statistical power were similar to those of other studies that correlated relative bite force with relative dewlap size (i.e., Vanhooydonck et al. 2005a; Lailvaux and Irschick 2007; Cox et al. 2009), an increase in sample size would have increased the power of our analyses, hence, might have affected our results on an association between the slopes and SSD or DI. Moreover, one can also question the validity of SSD as a measure of the intensity of intrasexual selection. Indeed, it has long been pointed out that SSD may also arise as a consequence of natural selection for reduction of food competition (Darwin 1871) or on clutch size in females (Tinkle et al. 1970). Reassuringly, several

studies have found that among-species variation in SSD correlates positively with other aspects of sexual dimorphism (such as dichromatism: Pérez I de Lanuza et al. 2013; Chen et al. 2012; Dale et al. 2015), indicating that SSD is at least to some extent under sexual selection. In a comparative analysis of almost 500 lizard species, Cox et al. (2003) did find significant correlations between SSD and female home range ratio and female home range size, two widely accepted proxies for the strength of intrasexual selection. In *Anolis*, the use of SSD as an indirect measure of sexual selection intensity has a long tradition (e.g., Trivers 1976; Stamps 1983), although several studies have suggested that variation in SSD may be driven by natural selection as well (e.g., Rand 1967; Losos et al. 2003). In a recent study on our study species *A. sagrei*, for example, Bonneaud et al. (2016) reported that resource availability can highly influence the degree of SSD among insular populations distributed across the Bahamas. Furthermore, paternity studies on *A. sagrei* proved that sexual selection is not uniformly directional with respect to male size and, therefore, fails to fully explain the observed male-biased SSD (Calsbeek and Sinervo 2004; Cox et al. 2007). Thus, the use of SSD here as metric for sexual selection is disputable. Besides, DI may be a rather “gross” proxy for the degree of intrasexual selection on each island population, because *A. sagrei* males may exhibit displays in various contexts (Driessens et al. 2014). Clearly, data on reliable estimates of the intensity of sexual selection are required. Some authors have advocated the use of sex ratios (e.g., Stamps 1983; Muralidhar and Johnson 2017), but others have warned that it is unsure to what extent observed sex ratio reflects operational sex ratio (the ratio of breeding males to breeding females, Cox et al. 2003). Other options include behavioral observations (e.g., number or duration of male–male aggressive interactions) and distributional data (territory size, overlap, number of females per territory, encounter rates; Johnson et al. 2009; Kamath and Losos 2018), but obtaining such data for many populations requires substantial time and effort, which probably explains why, after 50 years of research on anoles, such data remain largely unavailable (Losos et al. 2003).

SSD and DI cannot explain differences in the relationship between relative dewlap size and bite force among populations, but what other factors potentially can? One possible explanatory factor may involve intrapopulation variation in body size and the idea that relative indices become particularly important in populations where opponents match more often in body size. Transferring information on body

size is likely the first and most crucial step in the assessment game (e.g., Tokarz 1985; Hardy and Briffa 2013), as we already stated in the previous paragraph. However, when males of similar body size encounter each other, dewlap size might become the major signal for advertising fighting capacity. In support of this idea, we would expect relative dewlap size to become a more reliable signal of bite force when variation in body size decreases across populations. We could simply test this prediction with available data by regressing the slope of the relative dewlap size–bite force relationship against variance in body size across populations. Our data did not support the proposed idea (pgls regression: coefficient b variance SVL, $R=0.26$, $df=16$, $P=0.317$), perhaps because encounters between size-matched opponents may not occur that frequently. Moreover, previous studies have shown that when opponents are more similar in size, fights are more likely to escalate (as opposed to merely opponent assessment) and the outcomes harder to predict (Rand 1967; Molina-Borja et al. 1998; Panhuis and Wilkinson 1999). This might challenge the view that honest signals play a major role in the advertisement of fighting capacity during agonistic encounters between size-matched males.

Another factor that has recently been reported to affect the relationship between relative dewlap size and bite force is resource availability. Particularly, Lailvaux et al. (2012) showed that under limiting resource conditions, the honest dewlap size–bite force relationship in *A. carolinensis* gets disrupted. To put this idea to the test, we assessed whether variation in body condition (an estimate for resource availability) could explain the variation in the relative dewlap size–bite force relationship observed within *A. sagrei*. Indeed, we obtained a significant association with body condition (pgls regression: coefficient $b \sim$ body mass normalized for SVL, $R=0.62$, $df=16$, $P=0.009$). However, the correlation was negative and, therefore, opposes the findings reported by Lailvaux et al. (2012). We found that for *A. sagrei* males, dewlap size in itself becomes a more reliable signal of bite force in populations where males are in worse body condition (the relationship with body condition was not significant when using the absolute dewlap size–bite force relationships, $P=0.575$). Overall, we suggest that body size remains, independent of resource availability, the key predictor during opponent assessment. Yet, when males of similar body size encounter each other, the use of dewlap size to honestly signal fighting capacity might be particularly important for *A. sagrei* males in poor body condition. We believe

that males in poor body condition will suffer more from the exhaustion and injuries related to physical fights than *A. sagrei* males in normal or good body condition. Accordingly, in populations where males have a low body condition, the strong need to avoid escalated fights and thus, to precisely assess a size-matched opponent, might be higher (Andersson 1994; Maynard-Smith and Harper 2003). This may explain why dewlap size becomes a more reliable predictor of bite force in such populations. In contrast, males under high resource conditions might directly engage in physical fights when encountering a size-matched opponent (Rand 1967; Molina-Borja et al. 1998). Of course, future experiments are needed to confirm our suggestions and to provide additional evidence that resource availability, indeed, influences the correlation between relative dewlap size and bite force in *A. sagrei*.

Last, several other factors have been found to explain variation only in dewlap size and can as such, also affect the relation between signal size and performance trait. For example, Vanhooydonck et al. (2009) revealed that *A. sagrei* males had relatively larger dewlaps in populations where curly-tailed lizards (*Leiocephalus carinatus*), known to predate on anoles, are present. In that same study was also reported that relative dewlap size increased with SSD. Also hormone levels (i.e., testosterone) are proven to change dewlap size in *A. sagrei* males (Cox et al. 2009) and can, due to fluctuating levels, affect the relationship between dewlap size and bite force throughout seasons. In accordance, a previous study on *A. carolinensis* has shown that dewlap size is only a reliable signal of bite force during the breeding season, and not during winter (Irschick et al. 2006). Following Lailvaux and Irschick (2007), we sampled our *A. sagrei* populations during the breeding season, with the exception of one (i.e., population from San Salvador). Results from that latter population did not markedly deviate from the other study populations, indicating that the dewlap–bite force relationship in *A. sagrei* might not be significantly affected by season. Yet, experiments assessing the link between dewlap size and bite force in the same *A. sagrei* individuals throughout the year are needed to accurately assess seasonal effects.

Conclusion

To our knowledge, this is the first study showing evidence for a link between relative dewlap size and bite force within *A. sagrei* populations, during the breeding season. Based on our results, we suggest that dewlap size in *A. sagrei* males is in general a

redundant signal for body size in the advertisement of fighting capacity (absolute indices), but only in particular cases a direct signal of bite force (relative indices). Our study makes an important contribution by showing that the relationship between signal size and performance trait can differ substantially within one species. We therefore suggest that the use of only one population is not sufficient to draw general conclusions for a whole species, in this respect. Several factors (e.g., degree of territoriality, resource availability, season) are already known to affect the correlation between dewlap size and bite force; however, additional research is needed to shed more light on how these factors exactly affect this relationship.

Acknowledgments

We acknowledge S. De Decker, J. Harvey, A. Herrel, J. Husak, P. Maillis, J. Mertens, J.J. Meyers, D. Norris, V. Rivalta, L. Schettino, E. Schramme, B. Scott-Edwards, M. Valley, and L. Vandervorst for help during data collection. We further thank G. Reynolds for his useful advice regarding phylogenetic analyses, S. Van Dongen for statistical assistance, and two anonymous reviewers for significantly improving drafts of this manuscript.

Funding

This work was supported by the Belgian American Education Foundation (BAEF) [to S.B. a postdoctoral fellow]. This study was financed by an FWO-FL research grant [to T.D., an aspirant doctoral fellowship]. K.H. is a postdoctoral fellow of FWO-FL. Additional expenses for field missions were provided by Leopold III fund and the University of Antwerp (DOCOP). All work was carried out in accordance with the local Environmental Agencies and the University of Antwerp animal welfare standard and protocols (ECD 2011-64).

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