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Signal size allometry in *Anolis* lizard dewlaps

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Positive allometry of signalling traits has often been taken as evidence for sexual selection. However, few studies have explored interspecific differences in allometric scaling relationships among closely related species that vary in their degree of ecological similarity. *Anolis* lizards possess an elaborate retractable throat fan called a dewlap that is used for visual communication and differs greatly in size and colour among species. We observed that *Anolis* dewlaps demonstrate positive allometry: relative dewlap size increases with body size. We also observed that coexisting species are divergent in signal size allometries, while convergent species—similar in other aspects of ecology, morphology and behaviour—typically share similar dewlap allometric scaling relationships. These patterns suggest that dewlap scaling relationships may follow the same pattern as other traits in the anole radiation, where ecologically different sympatric species have evolved a suite of divergent traits.

1. Introduction

Visual signals represent some of the most elaborate biological features on Earth. From peacock tail feathers to fiddler crab claws, signalling traits have evolved to convey a range of information during visual communication [1–3]. Such traits often exhibit positive static allometry [4], whereby signal size is disproportionately larger with increasing body size [5]. As signalling traits have often been considered to influence reproductive fitness [4], positive allometric scaling of signal size has often been taken as evidence for sexual selection, although this has attracted some debate [4,6]. However, most studies have only explored allometric scaling in single species [5]; comparative studies that explore interspecific differences in signal size allometry among closely related species are rare (although see [7]).

In lizards, extendable throat fans called dewlaps have independently evolved in multiple lineages as a signal for visual communication [8,9]. The most speciose clade is *Anolis* lizards (anoles), in which sexual dimorphism in dewlap size is typical and male anoles usually possess relatively larger dewlaps than females [10]. However, evidence for positive allometry is mixed and comparative analyses are rare [11–14].

Anoles have independently radiated into convergent communities comprised of species specialized to use different portions of the structural environment (‘ecomorphs’; [15]) on each of the four large islands of the Greater Antilles: Cuba, Hispaniola, Jamaica and Puerto Rico [16]. Co-occurring species of different ecomorph classes rarely have dewlaps comprised of similar colours or patterns [14], which suggests a role for dewlaps as signals for species recognition ([17–19], but see [20]). However, members of the same ecomorph class, though convergent in ecology, morphology and behaviour, rarely are convergent in dewlap phenotype [14,20]. Comparative studies of dewlap size allometry, among either convergent species of the same ecomorph class or co-occurring species of different ecomorph classes, have been surprisingly overlooked.

Here, we explore three questions: (1) is there positive allometric scaling of dewlap size in *Anolis* lizards? (2) Do co-occurring species differ in signal size allometry? And (3) do convergent species have similar signal size allometry?

Table 1. Allometric relationships between dewlap size and body length in 10 *Anolis* lizard species. Slopes greater than 1 represent positive allometry where signal size (dewlap area) is disproportionately larger with increasing body size; *p*-values reflect a statistical difference of *b* to isometry (i.e. 1).

ecomorph	species	country	location	*N*	slope (*b*)	s.e.	R^2	*p*-value
trunk	*A. brevirostris*	Dom. Rep.	Barahona	118	1.108	0.149	0.324	0.469
trunk	*A. distichus*	Bahamas	Andros Island	47	1.255	0.264	0.335	0.338
trunk–crown	*A. grahami*	Jamaica	Long Mountain	103	1.453	0.094	0.703	<0.001
trunk–crown	*A. coelestinus*	Dom. Rep.	Barahona	39	1.486	0.078	0.907	<0.001
trunk–crown	*A. smaragdinus*	Bahamas	Andros Island	32	1.787	0.249	0.632	0.004
twig	*A. angusticeps*	Bahamas	Andros Island	52	1.800	0.290	0.436	0.008
twig	*A. valencienni*	Jamaica	Long Mountain	53	1.337	0.078	0.853	<0.001
trunk–ground	*A. cybotes*	Dom. Rep.	Barahona	73	1.771	0.106	0.797	<0.001
trunk–ground	*A. sagrei*	Bahamas	Andros Island	89	2.316	0.083	0.900	<0.001
trunk–ground	*A. lineatopus*	Jamaica	Long Mountain	261	2.426	0.064	0.849	<0.001

2. Methods

(a) Species sampling and field collection

Between 6 April–3 June and 2 November–16 December 2019, we sampled male *Anolis* lizards (table 1) in three communities: Jamaica (Long Mountain, Kingston), the Dominican Republic (Barahona province) and the Bahamas (Andros Island). In all communities no two species are of the same ecomorph class, and members of the same ecomorph class in different communities are not closely related (with the exception of *A. distichus* and *A. brevirostris*).

(b) Measurement of dewlap size

Dewlap size (total area) was calculated from digital photographs obtained in the field. Dewlaps were extended via pulling of the hyoid bone using a pair of small forceps (see electronic supplementary material, figure S1) and digital photographs were taken (Canon EOS Rebel T5 with X-Rite ColorChecker Passport for scale). We used a digital drawing tablet (Wacom Intuos Pro) to manually trace dewlaps in ImageJ [21] (all by B.K.). Body size (snout-to-vent length; SVL) was measured in the field using digital calipers (Mahr EWRi digital caliper; all by J.T.S.).

(c) Statistical analyses

Allometry describes the size of morphological traits relative to each other, most typically to body size. Specifically, allometric slopes (b) can be described using the equation $Y = aX^b$, where Y in our study represents dewlap size and X represents body size. Dewlap size (area) was first linearized with respect to body size (SVL) by square-root transformation and then both variables were natural log transformed [5,14]. Ordinary least squares regressions were used to determine allometric scaling relationships [5,14]. Isometry ($b = 1$) describes a relationship where relative trait size is constant with increasing body size. Positive allometry ($b > 1$) represents increasing relative trait size with body size; negative allometry ($b < 1$) describes the opposite. We used t-tests to investigate whether allometric slopes differed statistically from isometry. To test for divergence in static allometries (i.e. intraspecific relationships between variation in dewlap and body size) between co-occurring species in different ecomorph classes and convergence in static allometries between non-coexisting species of the same ecomorph class, we included a dewlap size × species interaction in independent multiple regression models for each community and ecomorph class. All analyses were conducted in R [22] using RStudio [23].

3. Results

(a) Static allometry of dewlap size

We sampled the dewlap sizes of 867 lizards. All species exhibited positive allometric scaling of dewlap size relative to body size (i.e. $b > 1$). Trunk–ground anoles exhibited the strongest allometry, while trunk anoles exhibited the weakest (and did not differ statistically from isometry; table 1, figure 1).

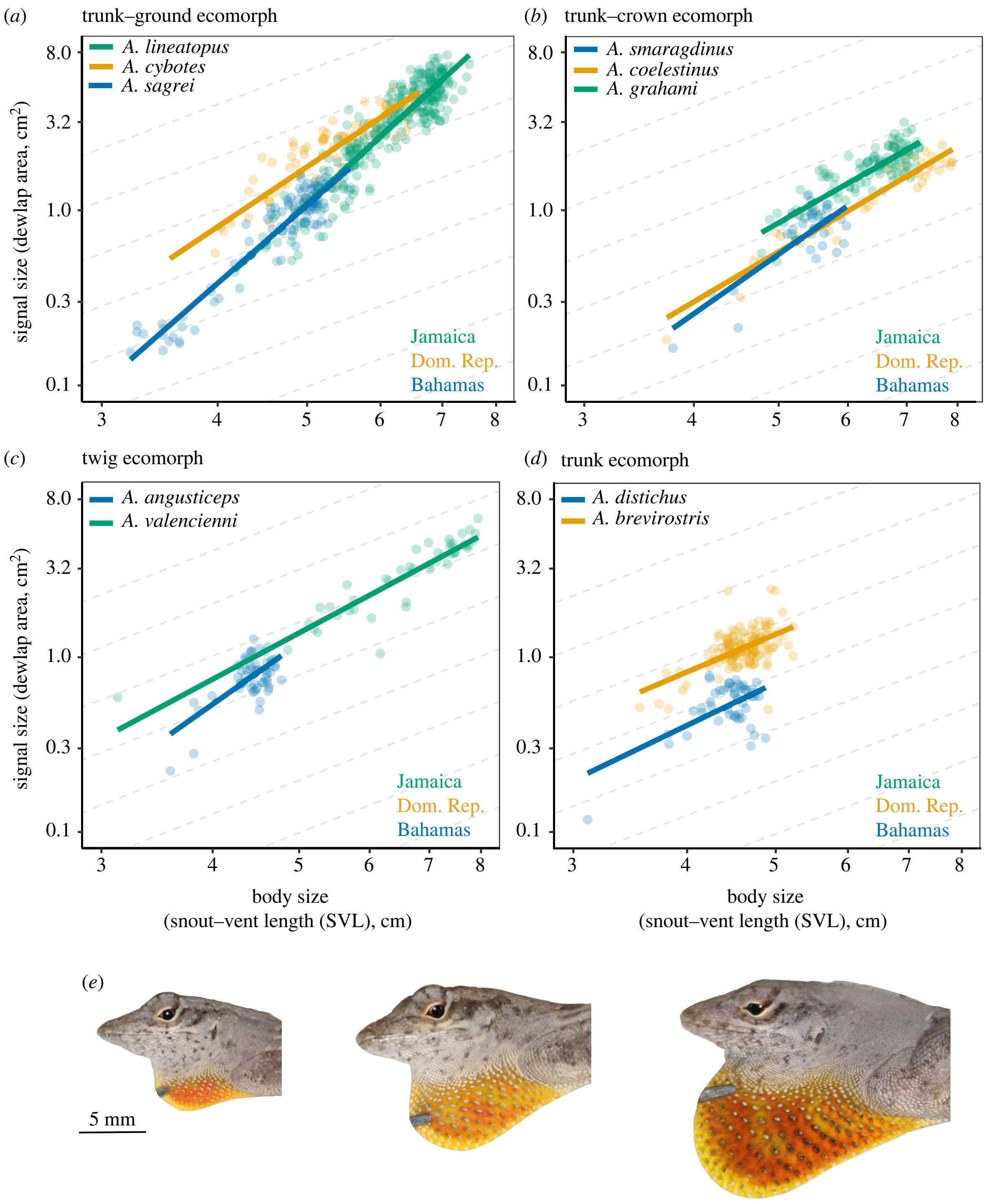
(b) Comparative analyses of dewlap size allometry

In all communities, co-occurring species exhibited different allometries of dewlap size (table 2). Between communities, species of the same ecomorph class typically exhibited similar allometries (table 2). Trunk–ground anoles were an exception: the allometric slope of *A. cybotes* was lower than that of both *A. sagrei* ($F_{1,158} = 60.8$, $p < 0.001$) and *A. lineatopus* ($F_{1,158} = 29.9$, $p < 0.001$). The removal of small-bodied outliers in both *A. distichus* and *A. valencienni* did not change overall results (see electronic supplementary material).

4. Discussion

All *Anolis* lizards in our study exhibited positive allometry in dewlap size (table 1 and figure 1). Specifically, we observed that dewlap allometry is very similar for allopatric species of the same ecomorph class (figure 1 and table 2*b*), but that co-occurring species—those of different ecomorph classes—vary significantly in dewlap size allometry (table 2*a*).

As positive signal allometry is often taken as evidence for sexual selection [4], interspecific differences in dewlap allometry may result from divergent sexual selection pressures. A comparative analysis of *Anolis* social behaviour found high variation among different ecomorphs in dewlap display rates and spatially structured social landscapes (e.g. interaction frequency of adult males overlapping in space; [24]). For example, male trunk–ground anoles spatially overlap with six times as many males as twig anoles but encounter a similar number of females [24]. These differences may lead to variable sexual selection pressures, driving evolutionary differences in dewlap allometry. Conversely, species of the same ecomorph



small lizard
(35 mm SVL)

medium lizard
(42 mm SVL)

large lizard
(49 mm SVL)

Figure 1. (*a–d*) Allometric scaling patterns of dewlap size in *Anolis* lizard ecomorphs. Positive allometry occurs when slopes are steeper than isometric dashed lines (i.e. $b = 2$, as dewlap area data presented here are not linearized). (*e*) Typical dewlap size progression with body size in *Anolis sagrei*.

class are typically very similar in social [24] and dewlap attributes (table 2, [20]). In the same vein, convergence within ecomorphs could result from similar sexual selection pressures. For example, trunk–ground anoles typically exhibit the highest rates of dewlap display behaviours associated with courtship and competitive social conflict [24–26], suggesting strong sexual selection may occur. Concomitantly, trunk–ground species in our study displayed the steepest allometric slopes of dewlap size (table 1).

Sexual selection is not the only factor affecting dewlaps, however; rather, dewlaps are multi-purpose signals, communicating information not only to male rivals [27] and potential mates [28,29], but also congeneric competitors [17] or even predators [30,31]. Therefore, while dewlap traits may have direct reproductive fitness consequences through their function in courtship interactions, as well as many indirect fitness consequences, the relative importance of these biotic interactions could be expected to differ among ecomorphs classes that inhabit different parts of the structural environmental and differ in behaviour and social structures [24]. The variation in dewlap allometry that we observed could have evolved due to this variation in function: species with social systems where signals function primarily for courtship often have different optimal allometric slopes than those that

Table 2. Differences in allometric scaling of dewlap size in (a) co-occurring species of different ecomorph classes and (b) convergent but allopatric species of the same ecomorph class.

	sum sq.	d.f.	*F*	*p*
(a) *ecomorph differences within a community*				
Jamaica × ecomorph	1.37	2,411	67.05	<0.001***
Bahamas × ecomorph	0.24	3,212	7.15	<0.001***
Dom. Rep. × ecomorph	0.14	2,224	7.07	0.001**
(b) *ecomorph similarities between communities*				
trunk × species	<0.01	1,161	0.28	0.595
trunk–ground × species	0.25	2,411	11.12	<0.001***
(*A. cybotes* excluded)	0.01	1,343	0.90	0.344
trunk–crown × species	0.02	2,168	1.26	0.285
twig × species	0.03	1,106	2.64	0.107

function as threat displays [32]. The patterns of dewlap size allometry that we observed—both the divergence in sympatry and convergence within ecomorphs—are likely the result of a complex trade-off between the multiple functions of the dewlap (e.g. courtship and antagonism) which may vary among ecomorphs.

While dewlap phenotypes likely evolve primarily due to the dual roles of signalling behaviours that have both direct (i.e. courtship) and indirect (e.g. mediation of agonistic interactions among competing males) fitness effects, the context of communication between the signaller and the receiver may also play a major role [33]. In anoles, it is likely that dewlap size is a proxy for overall body size (as the two are highly correlated; table 1). However, variation in the strength of this correlation—as well as the allometric slope—exists among ecomorphs. One possible explanation is due to variation in signalling distance among ecomorphs. *Anolis* visual systems are complex, possessing fovea that facilitate binocular visual acuity [34–36], and are very similar among species [37,38], suggesting little interspecific variation in visual acuity as it pertains to distance [39]. As small differences in absolute size are more difficult to discern with increasing distance [40], species that display from further distances would be expected to have allometric slopes that are both steeper and more highly correlated. In this way, increased allometry would exaggerate the signal's message while increased correlation would increase the signal's accuracy. Trunk–ground anoles have the largest dewlaps of all ecomorphs [41] and also display from greater distances and in environments with the fewest visual obstructions [24,26]; our results suggest that these species also exhibit the strongest positive allometry in dewlap size and dewlaps most accurately represent body size (table 1). The strength of allometry in dewlap size may therefore be a function of the distance at which different species communicate, with allometric slopes being strongest in those that display from the greatest distance.

Allometric scaling patterns may also be affected by the viability costs associated with dewlap size, which may vary among microhabitats and so among ecomorphs. However, comparative data on viability among *Anolis* ecomorphs are lacking but would be exceptionally valuable in clarifying these dynamics.

A recent study of dewlap size allometry in Caribbean anoles reported surprising evidence for *hypo*-allometry, i.e. dewlap size was proportionately *smaller* with increasing body size [14]. This result was especially surprising as it was counter to all other studies (e.g. [11–13]), including our results here. The paper introduced a new method based on measurements taken from videos of lizards displaying in nature [14]. Though an innovative and potentially important method, when we examined the underlying data associated with the paper, we found that the dewlap size measurements are vastly larger than our measurements of individuals of the same species (see electronic supplementary material). These video-derived size estimates were not validated by additional measurement methods (e.g. the methods used in this article) and so their accuracy remains unclear. Further studies using such video-based measurements of anole dewlaps would benefit from detailed validation of the accuracy of trait size estimates before such studies can challenge the results consistently discovered by other studies of anole dewlap allometry.

Here, we observed that all *Anolis* species exhibit positive allometry in dewlap size: larger individuals had proportionately larger dewlaps for their body size than small individuals, although the strength of this allometry varied among species. As our study represents one of the first comparative analyses of signal size allometry in lizard dewlaps, it remains unclear if these patterns are specific only to anoles or are consistent across in the multiple independent lineages that have evolved dewlap structures [8,9].

Ethics. All research was conducted in accordance with Washington University IACUC no. 20180101.

Data accessibility. Raw data included as electronic supplementary material.

All data associated with this study are included as electronic supplementary material [42].

Authors' contributions. J.T.S.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualization, writing—original draft and writing—review and editing; A.P.: investigation, writing—original draft and writing—review and editing; B.K.: data curation, formal analysis, investigation and writing—review and editing; K.W.: data curation, investigation and writing—review and editing; J.J.S.: data curation, investigation and writing—review and editing; J.B.L.: formal analysis, funding acquisition, resources, supervision and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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