

What determines dewlap diversity in *Anolis* lizards? An among-island comparison

B. VANHOODYDONCK,* A. HERREL,* † J. J. MEYERS‡ & D. J. IRSCHICK‡

*Department of Biology, University of Antwerp, Antwerp, Belgium

†Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA

‡Department of Biology, University of Massachusetts, Amherst, MA, USA

Keywords:

interpopulation variation;
natural selection;
sexual selection;
signals;
species recognition.

Abstract

Animal signalling systems are extremely diverse as they are under different, often conflicting, selective pressures. A classic textbook example of a diverse signal is the anoline dewlap. Both at the inter- and intraspecific levels, dewlap size, colour, shape and pattern vary extensively. Here, we attempt to elucidate the various factors explaining the diversity in dewlap size and pattern among seven *Anolis sagrei* populations from different islands in the Bahamas. The seven islands differ in the surface area, number and kind of predators, sexual size dimorphism and *Anolis* species composition. In addition, we investigate whether selective pressures acting on dewlap design differ between males and females. Whereas dewlap pattern appears to serve a role in species recognition in both sexes, our data suggest that relative dewlap size is under natural and/or sexual selection. We find evidence for the role of the dewlap as a pursuit-deterrence signal in both males and females as relative dewlap size is larger on islands where *A. sagrei* occurs sympatrically with predatory *Leiocephalus* lizards. Additionally, in males relatively large dewlaps seem to be selected for in a sexual context, whereas in females natural selection, for instance by other predators than *Leiocephalus* lizards, appears to constrain relative dewlap size.

Introduction

As they are extremely diverse and often conspicuous, animal signals have long intrigued evolutionary biologists (review in Bajema, 1984). A myriad of factors are known to drive the evolution of signalling systems but processes thought to be responsible for signal diversity can generally be classified either as stochastic processes or selective processes. In contrast to stochastic events, selection pressures are continuously acting on natural populations. Natural and sexual selective pressures, however, may pose conflicting demands on the signalling system. For a signal to be effective in a sexual context, it needs to be conspicuous to conspecifics. Large, elaborate signals, however, often also draw the unwanted atten-

tion of predators and cryptic signals will be favoured in this context. Signal design can thus be seen as the evolutionary balance between natural and sexual selection acting on the system at any given moment (Endler, 1983, 1992; Andersson, 1994; Zuk & Kolluru, 1998).

Besides natural and sexual selection in the strictest sense, a third, nonmutually exclusive hypothesis has often been put forward as driving signal diversity. The species recognition hypothesis suggests that obvious signals are selected for by the need for rapid unambiguous identification of species by conspecifics, thus avoiding costly mating errors (Figueroa & Green, 2000; Seddon, 2005; Ord & Martins, 2006). If so, sympatric species can be expected to possess more distinct and easily distinguishable signals than allopatric species (Butcher & Rohwer, 1989; Price, 1998; Figueroa & Green, 2000). For instance, in antbirds the songs of closely related sympatric pairs of species are more divergent than those of allopatric pairs (Seddon, 2005).

Correspondence: Bieke Vanhooydonck, Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Antwerp, Belgium.
Tel.: + 32 3 820 2293; fax: + 32 3 820 2271;
e-mail: bieke.vanhooydonck@ua.ac.be

The *Anolis* dewlap represents a textbook example of a diverse signal. The dewlap is a characteristic feature of *Anolis* lizards and consists of an extendable flap of skin attached to the lizards' throat. Although the dewlap is suggested to play an important role in male–male interactions, female choice, pursuit-deterrence and/or species recognition (Greenberg & Noble, 1944; Williams & Rand, 1977; Echelle *et al.*, 1978; Fitch & Hillis, 1984; Losos & Chu, 1998; Leal, 1999; Jenssen *et al.*, 2000; Lailvaux & Irschick, 2007; Nicholson *et al.*, 2007), the function and the evolution of the dewlap remain largely a mystery. Among *Anolis* species, dewlap design, i.e. size, shape, colour and pattern is extremely diverse, with many species having uniquely designed dewlaps that are used to delineate species (Nicholson *et al.*, 2007 and references therein).

In addition to being extremely diverse at the inter-specific level, anoline dewlap design also varies greatly within and among different populations of the same species (Echelle *et al.*, 1978; Leal & Fleishman, 2004; Vanhooydonck *et al.*, 2005a). That dewlap design may be as variable within as among species is evidenced by the fact that among the seven *Anolis sagrei* populations we sampled, four out of the six dewlap pattern categories described for different *Anolis* species (Nicholson *et al.*, 2007) occur (Fig. 1). As intraspecific, among-population differences may represent incipient stages of speciation (Foster *et al.*, 1998), examining them may reveal mechanisms responsible for the diversity in dewlap design for the entire *Anolis* radiation. Also, as the strength of selective processes typically varies geographically, the relative contribution of natural and sexual selection to the variation in signal design may be elucidated by population comparisons (Foster, 1999). Studies on a range of taxa corroborate the idea that interpopulational variation in signal design reflects the differential balance between natural and sexual selection pressures (insects: Lewkiewicz & Zuk, 2004; Svensson *et al.*, 2006; fish: Endler, 1992; Moyaho *et al.*, 2004; Hamon & Foote, 2005; Millar *et al.*, 2006; reptiles: Macedonia *et al.*, 2002; Kwiatkowski, 2003; Stuart-Fox *et al.*, 2004; birds: Blondel *et al.*, 2002).

Here, we attempt to disentangle the various causes of variation in dewlap design (i.e. dewlap size and pattern) for seven populations of *A. sagrei* lizards from the Bahamas. In addition, we specifically examine whether selective pressures acting on dewlap design differ among males and females. Surprisingly, previous studies on anoline dewlap diversity have exclusively focused on male dewlap design (e.g. Echelle *et al.*, 1978; Losos & Chu, 1998; Nicholson *et al.*, 2007), yet in most anole species females also possess a dewlap. In nature, females extend and display their dewlaps, although they do so less frequently and in other contexts than males (Jenssen *et al.*, 2000; Lovern & Jenssen, 2001; Orrell & Jenssen, 2003). In addition, the female dewlap is typically smaller and less distinctly coloured than that of males (Jenssen

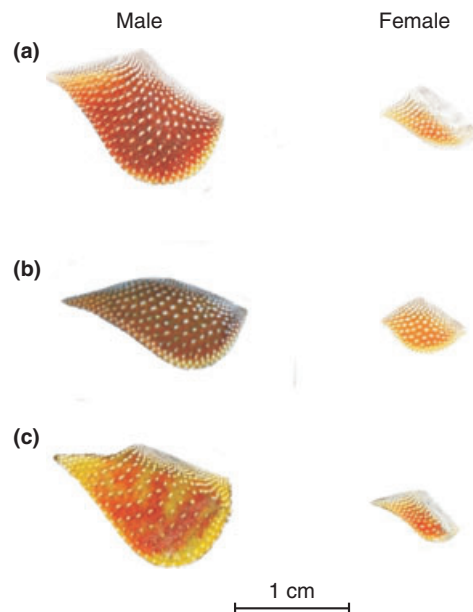


Fig. 1 Example pictures of dewlaps in male (left) and female (right) *Anolis sagrei* from (a) Crooked, (b) Staniel Cay and (c) Andros. Individuals are of similar snout–vent length. Male *A. sagrei* have larger dewlaps than females and *A. sagrei* lizards from Crooked, an island with *Leiocephalus carinatus* present, have relatively larger dewlaps than the ones from Staniel Cay, an island without *L. carinatus* present. Dewlap pattern in *A. sagrei* from Andros, a four-species island, is more complex (i.e. striped) than the dewlap patterns in *A. sagrei* from both Crooked, a two-species island, and Staniel Cay, a three-species island. Scale bar represents 1 cm.

et al., 2000). This suggests selective pressures on dewlap design may differ between the sexes (cf. Blanco & De La Puente, 2002; Vanhooydonck *et al.*, 2005a).

To ensure varying degrees of sexual and natural selection and congeneric competition acting on the different *A. sagrei* populations, we sampled each population on a different island in the Bahamas. The seven islands were selected so that they varied greatly in surface area, number and kind of predators, and *Anolis* species composition (Table 1). This work thus follows in the footsteps of other studies of island biogeography that examine how factors that change across different islands (e.g. predator profiles) affect various aspects of the organismal phenotype (reviews in Grant, 1998; Stuessy & Ono, 1998).

The number of sympatric *Anolis* species was used to test the species recognition hypothesis. On the different islands in the Bahamas, the number of sympatric *Anolis* species ranges from one to four (Losos *et al.*, 1994), providing a perfect natural laboratory to examine whether dewlap design is more distinct when more species occur sympatrically and where rapid, unambiguous identification of conspecifics is likely advantageous. As a measure of intensity of sexual selection, we used

Table 1 Data on number of individuals measured, island area, tail break frequency (TBF), presence/absence of *Leiocephalus carinatus* lizards (*Lc*, 0 = absent, 1 = present), and number of *Anolis* lizards per island and sex (M = male, F = female), where applicable.

Island	Sex	<i>N</i>	Island area (km ²)	TBF	<i>Lc</i>	No. <i>Anolis</i>	Dewlap size (mm ²)	Dewlap pattern	SVL (mm)
Pidgeon Cay	M	17	0.019	0.47	0	2	126.39 ± 10.24	0.92 ± 0.02	48.11 ± 1.13
	F	8		0.25			23.95 ± 1.25	1.00 ± 0.00	40.46 ± 1.04
Staniel Cay	M	27	5.18	0.37	0	3	162.90 ± 11.96	0.90 ± 0.02	52.29 ± 1.18
	F	21		0.33			21.91 ± 1.22	0.97 ± 0.01	39.48 ± 0.61
Chub Cay	M	22	15.76	0.32	1	4	145.61 ± 11.29	0.56 ± 0.03	47.60 ± 1.12
	F	21		0.38			19.86 ± 1.36	0.75 ± 0.03	35.82 ± 0.56
Crooked	M	24	238.28	0.46	1	2	166.66 ± 13.52	0.96 ± 0.01	50.17 ± 1.14
	F	19		0.48			26.07 ± 1.25	0.96 ± 0.02	40.19 ± 0.64
Acklins	M	11	310.8	0.55	1	2	217.77 ± 26.82	0.97 ± 0.01	55.69 ± 2.38
	F	12		0.09			27.63 ± 1.44	0.99 ± 0.01	40.11 ± 0.87
Grand Bahama	M	29	1373	0.54	1	3	131.05 ± 10.26	0.91 ± 0.01	43.38 ± 1.36
	F	23		0.38			16.73 ± 0.79	0.88 ± 0.02	33.88 ± 0.44
Andros	M	25	5957	0.50	0	4	110.23 ± 8.17	0.65 ± 0.03	46.63 ± 0.77
	F	18		0.45			18.25 ± 0.84	0.83 ± 0.03	37.52 ± 0.57

Also shown are the mean ± standard error of dewlap size, dewlap pattern and SVL per island and sex.

sexual size dimorphism. Sexual size dimorphism has been widely used as an indirect measure of sexual selection because there is strong evidence that it is associated with the ability to compete over mates, with mating systems, and with territoriality (Stuart-Fox & Ord, 2004; Ord & Martins, 2006; and references therein).

As a proxy for the strength of natural selection, we examined the following three variables: (i) island size, (ii) the occurrence of *Leiocephalus carinatus* lizards and (iii) tail break frequency. First, island size is typically correlated with the number of species inhabiting the island (MacArthur & Wilson, 1967; Losos & Schluter, 2000; Ricklefs & Bermingham, 2004), and the number of very large predators, such as raptorial birds, may be disproportionately lower on small islands (Schoener & Schoener, 1978, 1982; McLaughlin & Roughgarden, 1989). Specifically, in the Bahamas, annual survival of *Anolis sagrei* is lower on large islands with a more diverse avifauna, thus suggesting increased levels of predation, and stronger natural selection on large islands when compared with small islands (Schoener & Schoener, 1978). In addition, the presence of *L. carinatus* lizards may have both direct (e.g. predation) and indirect (e.g. competition for food) effects on the survival of *Anolis* lizards in the Bahamas (Schoener *et al.*, 1982, 2002), thus increasing the intensity of natural selection on islands where *Leiocephalus* and *Anolis* lizards occur in sympatry. Third, tail autotomy is a common antipredator mechanism among lizards (Pough *et al.*, 2001). Although it has been intensely debated whether it actually reflects the intensity of predation or the inefficiency of predators (Schoener & Schoener, 1980; Turner *et al.*, 1982; Jaksic & Greene, 1984; Fox *et al.*, 1994), tail break frequency has been used as an indicator of predation pressure in other lizard species (Kwiatkowski, 2003).

Specifically, we test whether the among-island variation in two aspects of dewlap design (i.e. size and pattern)

in *A. sagrei* can be best explained by the variation in different selective agents (i.e. natural selection, sexual selection, species recognition), separately or in combination. Second, we test whether similar selective pressures act on dewlap design in male and female *A. sagrei*.

Material and methods

Animals

Between 24 April 2003 and 18 May 2003, we visited seven different islands in the Bahamas (i.e. Andros, Grand Bahama, Chub Cay, Staniel Cay, Pidgeon Cay, Crooked and Acklins) and captured a total of 277 adult *A. sagrei* lizards by hand or noose. We measured snout–vent length (SVL) of all captured individuals to the nearest 0.01 mm using digital callipers (Mitutoyo CD-15DC; Mitutoyo [UK] Ltd., Telford, UK). In addition, we noted the sex of each individual and the condition of its tail (i.e. regenerated or not).

For six of the seven islands we visited, information on island area was readily available from the literature (Losos *et al.*, 1994), or on the world wide web (<http://www.geographia.com/bahamas/map.htm>). We estimated the area of Pidgeon Cay by comparing its size to the known size of Staniel Cay, which is the neighbouring island, on an aerial image provided by Google Earth. Based on the available literature (Schwartz & Henderson, 1991) and personal observations, we noted whether *L. carinatus* lizards were present (Table 1).

To be able to test the species recognition hypothesis (see Introduction), we also sampled the co-occurring *Anolis* species on each island. Specifically, *Anolis carolinensis* occurs on all seven islands and 167 adult individuals were captured in total. *Anolis distichus* occurs on Andros, Chub Cay, Grand Bahama and Staniel Cay, whereas *Anolis angusticeps* occurs only on the former two. In total,

we captured 78 and 83 adult individuals of each species respectively. Of all these individuals, we noted its sex and took a digital picture of the dewlap (see below).

Dewlap measurements

To obtain a reliable measure of dewlap size, we positioned the lizard sideways and pulled the base of the second ceratobranchial gently forward with a pair of forceps. As the dewlap consists of a skin flap attached to the lizard's throat on the one side and to the hyoid bone on the other, the dewlap becomes maximally extended when the ceratobranchial is pulled forward completely (see Bels, 1990). After positioning the lizard in such a way that its extended dewlap was parallel to the lens of the camera (Nikon Coolpix 4500; Nikon Inc., Chicago, IL, USA), we took a digital picture. We placed a tape measure (accuracy of 1 mm) next to the extended dewlap to provide a scale. Using the program `TRSDIG` (v. 1.39; J. Rohlf, SUNY, Stonybrook, NY, USA), we digitized the outer edge of the dewlap and calculated total dewlap size for each individual. This method of measuring dewlap size yields highly repeatable results (Vanhooydonck *et al.*, 2005b). For those dewlaps that consisted of two differently coloured parts (i.e. visible to the human eye), we subsequently delineated the part of the dewlap that consisted of the main colour using the same program. If spots or stripes were present, we digitized around their outer edges. As a measure of dewlap patterning, we used the ratio of the area covered by the main colour to the total dewlap size. This measure corresponds to the different categories of dewlap patterns found among *Anolis* species as described by Nicholson *et al.* (2007). The highest ratio (i.e. ratio of 1) represents the solid dewlap, the lowest ratio the spotted dewlap. The three ratios in between represent in decreasing order, the marginal, basal and striped dewlap. All *A. carolinensis* and *A. angusticeps* we captured possessed a solid dewlap, whereas *A. sagrei* and *A. distichus* showed a great diversity in dewlap patterns. We captured *A. sagrei* individuals possessing solid, marginal, basal and striped dewlaps and *A. distichus* individuals possessing solid, marginal, basal and spotted dewlaps (cf. Nicholson *et al.*, 2007). Neither in male nor female *A. sagrei* are dewlap pattern and relative dewlap size significantly correlated ($r = 0.26$, $P = 0.58$; $P = 0.12$, $P = 0.79$ respectively).

Statistics

We used `SPSS` (v 13.0) (SPSS Inc., Chicago, IL, USA) for all statistical analyses. Per island and sex, we calculated the mean dewlap size, dewlap pattern and SVL (Table 1). Sexual size dimorphism was calculated as the mean SVL in males divided by the mean SVL in females per island (cf. Butler *et al.*, 2000; Losos *et al.*, 2003). We calculated the ratio of number of individuals with a regenerated tail to the total number of individ-

uals captured per population and sex to get an estimate of tail break frequency (Table 1). Prior to statistical analyses, the mean dewlap size, mean SVL, sexual size dimorphism and island area were logarithmically (\log_{10}) transformed to make sure that they were normally distributed. We regressed, per sex, the mean dewlap size against mean SVL and calculated the residuals. Residual dewlap size was subsequently used in the analyses. Mean dewlap pattern and tail break frequency were arcsine transformed (Sokal & Rohlf, 1995). None of the bivariate correlations among the five covariates were significant (all $r < 0.57$, all $P > 0.18$).

We used an information theoretic approach to the model selection (Burnham & Anderson, 2002) to compare seven different plausible models of selection for both residual dewlap size and dewlap pattern. The first model was based on the sexual selection hypothesis and included sexual size dimorphism. The second model, based on the natural selection hypothesis, included island area, tail break frequency and absence/presence of *L. carinatus* lizards, as covariates. The third model was based on the species recognition hypothesis and included the number of *Anolis* lizards as covariate. The four remaining models were based on the combination of the different hypotheses (i.e. model 4: natural selection, sexual selection and species recognition; model 5: natural and sexual selection; model 6: natural selection and species recognition; model 7: sexual selection and species recognition). As our sample size (i.e. seven islands) is too low to include all five covariates in model 4 or four covariates in models 5 and 6, we decided to include only one of the natural selection-related covariates in these analyses. Which covariate was included, was based on the relative importance of each of the three covariates in the natural selection model. We calculated the importance of each covariate by summing the Akaike weights of the complete natural selection model and models including each of the covariates separately (see also below).

Specifically, we used the Akaike Information Criterion differences (Δ_i) to determine the likelihood that a given model is the best model among the candidate models. The best model has a Δ_i value of zero. Models with Δ_i values up to 2 have substantial empirical support, models with Δ_i values between 4 and 7 have considerably less support, and models with Δ_i values > 10 have essentially no empirical support (Burnham & Anderson, 2002). In addition, we used Akaike weights (w_i) to provide another measure of the strength of evidence for each model. Akaike weights (w_i) indicate the probability that a given model is the best among the whole set of candidate models (Burnham & Anderson, 2002). Thus, the best model has the lowest Δ_i value and highest w_i . We subsequently calculated the importance of the different variables included in the best model(s), by summing the Akaike weights for all models containing that particular variable. The variable with the largest summed weight

(w_+) is estimated to be the most important; the variable with the smallest sum is estimated to be the least important (Burnham & Anderson, 2004).

Both in males and females, the species recognition model turned out to be the best model of the seven candidate models to explain the variation in dewlap pattern (see Results). Thus, we subsequently compared the frequency distributions with regard to dewlap pattern among the co-occurring *Anolis* species. This way we aim at testing explicitly whether the changes we find in dewlap pattern in *A. sagrei* actually occur with respect to the dewlap pattern of the other sympatric *Anolis* species. We did so by performing a nonparametric Kruskal–Wallis test with dewlap patterning (per individual) as dependent and species as factor. Sexes and islands with different numbers of co-occurring *Anolis* species (i.e. 2, 3 or 4) were analysed separately. By combining the results of these analyses and the results of the model selection analyses outlined above, we get at the issue of character displacement with respect to dewlap patterning in *A. sagrei*.

Results

Relative dewlap size in males

Based on the summed Akaike weights, the absence/presence of *L. carinatus* lizards appeared to be the most important predictor variable in the natural selection model ($w_+ = 0.99$; island area and tail break frequency: $w_+ = 0.15$). Therefore, in all models combining the natural selection hypothesis with the sexual selection and/or species recognition hypotheses, we used the absence/presence of *L. carinatus* lizards as the sole natural selection-related covariate.

Of the seven alternative models for selection on male residual dewlap size in *A. sagrei*, the model including both the absence/presence of *L. carinatus* lizards on the island and degree of sexual size dimorphism has the lowest Δ_i value and highest w_i . The combined natural and sexual selection model has a 41% chance of being the best model (Table 2). Male *A. sagrei* occurring on islands with *L. carinatus* lizards have larger relative dewlaps than males occurring on islands without *L. carinatus* (Fig. 2a). Similarly, the degree of sexual size dimorphism is positively related to relative dewlap size among male *A. sagrei* (Fig. 2b). Still, the model based on a combination of the species recognition and natural selection hypotheses (i.e. model 6) and the model based on all three hypotheses (i.e. model 4) also have considerable empirical support ($\Delta_i < 2$, Table 2). Summing the Akaike weights for the different covariates in these models shows that the absence/presence of *L. carinatus* lizards is the most important predictor variable ($w_+ = 0.99$), followed by sexual size dimorphism ($w_+ = 0.57$). The number of congeneric species is the least important ($w_+ = 0.45$).

Dewlap pattern in males

In the natural selection model, tail break frequency appears to be the most important predictor variable ($w_+ = 0.71$), whereas the absence/presence of *L. carinatus* lizards and island area are the least important ($w_+ = 0.40$ and 0.39 respectively). We therefore introduced tail break frequency as the sole natural selection-related covariate in all combined models (i.e. models 4, 5 and 6).

Dewlap pattern in male *A. sagrei* seems to be mainly affected by the number of congeneric (i.e. *Anolis*)

Table 2 Akaike Information Criteria (AIC), AIC differences (Δ_i) and Akaike weights (w_i) of the seven alternative models explaining the variation in residual dewlap size and pattern among seven populations of male *Anolis sagrei* lizards.

Model	Covariates	AIC	AIC difference (Δ_i)	Akaike weight (w_i)
Residual dewlap size				
(1) Sexual selection	SSD	-22.06	10.96	0.002
(2) Natural selection	Island area, TBF, <i>Lc</i>	-30.84	2.18	0.137
(3) Species recognition	No. <i>Anolis</i>	-18.79	14.23	0.0003
(4) Sexual selection, natural selection and species recognition	SSD, <i>Lc</i> , no. <i>Anolis</i>	-31.20	1.81	0.165
(5) Sexual and natural selection	SSD, <i>Lc</i>	-33.02	0	0.407
(6) Natural selection and species recognition	<i>Lc</i> , no. <i>Anolis</i>	-32.32	0.69	0.288
(7) Sexual selection and species recognition	SSD, no. <i>Anolis</i>	-20.55	12.47	0.0007
Dewlap pattern				
(1) Sexual selection	SSD	3.05	13.50	0.0003
(2) Natural selection	Island area, TBF, <i>Lc</i>	1.88	12.33	0.0006
(3) Species recognition	No. <i>Anolis</i>	-10.45	0	0.283
(4) Sexual selection, natural selection and species recognition	SSD, TBF, no. <i>Anolis</i>	-10.29	0.16	0.261
(5) Sexual and natural selection	SSD, TBF	2.34	12.79	0.0004
(6) Natural selection and species recognition	TBF, no. <i>Anolis</i>	-9.80	0.65	0.205
(7) Sexual selection and species recognition	SSD, no. <i>Anolis</i>	-10.20	0.25	0.250

The model with the lowest Δ_i value and the highest w_i is considered the 'best' model among the candidate models (in bold). SSD, sexual size dimorphism; TBF, tail break frequency; *Lc*, absence/presence *Leiocephalus carinatus* lizards.

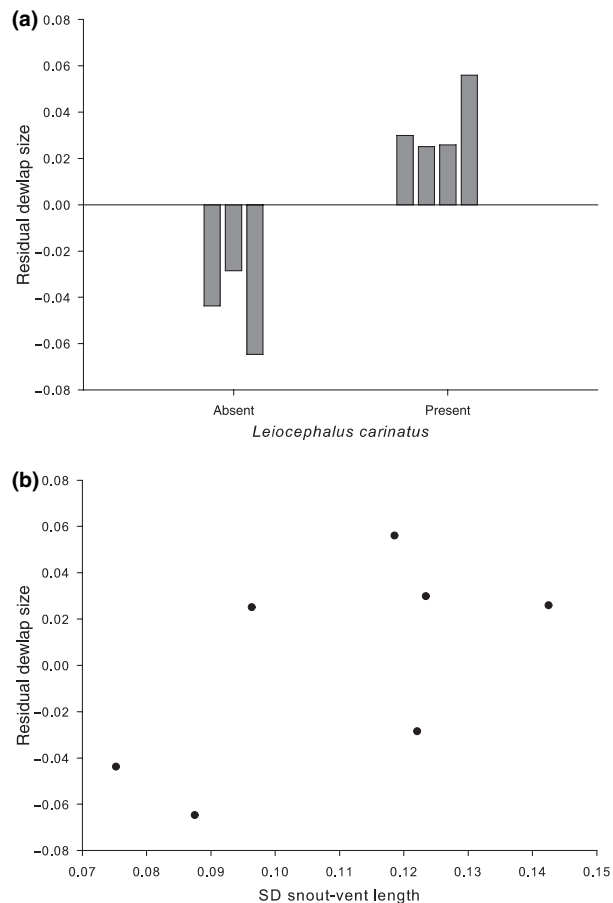


Fig. 2 Plot of male residual dewlap size against the covariates in the model with the lowest Δ_i and highest w_i of all alternative models: (a) absence or presence of *Leiocephalus carinatus* lizards ($w_+ = 0.99$) and (b) degree of sexual size dimorphism ($w_+ = 0.57$). Male residual dewlap size is larger on islands with higher levels of sexual dimorphism and on islands with *L. carinatus* present. Male residual dewlap size thus seems to be affected by both sexual and natural selection, acting in the same direction.

species as the model based on the species recognition hypothesis has the lowest Δ_i value and highest w_i of the seven candidate models. It has a 28% chance of being the best model. The more congeneric species co-occur on the same island, the more complex (i.e. smaller ratio of the area covered by the main colour to the total area) the pattern of the dewlap in male *A. sagrei* becomes (Fig. 3a). Still, the models combining the species recognition and natural selection hypotheses, the species recognition and sexual selection hypotheses, and all three hypotheses have substantial empirical support (all $\Delta_i < 2$, Table 2). Summing the Akaike weights of the different covariates included in these models, however, shows that the number of congeneric species is the most important predictor variable ($w_+ = 0.99$), followed by sexual size dimorphism ($w_+ = 0.51$). Tail break

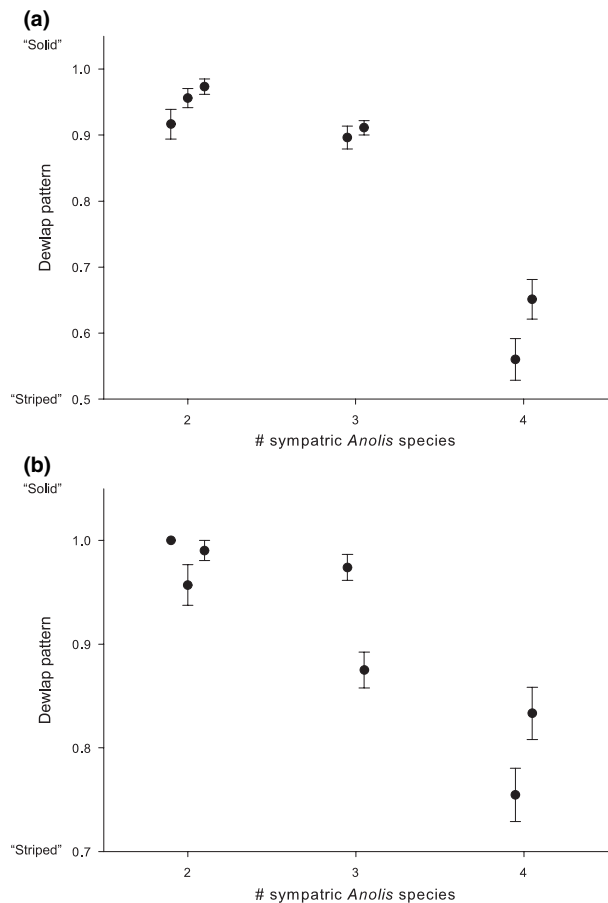


Fig. 3 Plot of dewlap pattern against the number of sympatric *Anolis* species in (a) males ($w_+ = 0.99$) and (b) females ($w_+ = 0.98$). Both in males and females, the model based on the species recognition hypothesis has the lowest Δ_i and highest w_i in comparison with the alternative models. Averages and standard error bars are shown per island. Data points are offset for clarity reasons. Dewlap patterns are more complex (i.e. striped pattern) on islands with more *Anolis* species present. Male and female dewlap pattern may thus function as a species recognition trait.

frequency is the least important predictor variable ($w_+ = 0.47$).

Relative dewlap size in females

Of the three covariates in the natural selection model, the absence/presence of *L. carinatus* lizards is the most important predictor variable ($w_+ = 0.99$), compared to island area and tail break frequency (both $w_+ = 0.98$). Therefore, the absence/presence of *L. carinatus* lizards was used as the sole natural selection-related covariate in subsequent combined models.

In female *A. sagrei*, the best model out of the seven alternatives to explain the variation in residual dewlap size was the one based on the natural selection hypo-

Table 3 Akaike Information Criteria (AIC), AIC differences (Δ_i) and Akaike weights (w_i) of the seven alternative models explaining the variation in residual dewlap size and pattern among seven populations of female *Anolis sagrei* lizards.

Model	Covariates	AIC	AIC difference (Δ_i)	Akaike weight (w_i)
Residual dewlap size				
(1) Sexual selection	SSD	-23.32	15.92	0.0003
(2) Natural selection	Island area, TBF, Lc	-39.24	0	0.873
(3) Species recognition	No. <i>Anolis</i>	-22.40	16.84	0.0002
(4) Sexual selection, natural selection and species recognition	SSD, Lc, no. <i>Anolis</i>	-34.10	5.14	0.067
(5) Sexual and natural selection	SSD, Lc	-29.28	9.96	0.006
(6) Natural selection and species recognition	Lc, no. <i>Anolis</i>	-33.62	5.62	0.053
(7) Sexual selection and species recognition	SSD, no. <i>Anolis</i>	-25.34	13.90	0.0008
Dewlap pattern				
(1) Sexual selection	SSD	1.09	10.22	0.002
(2) Natural selection	island area, TBF, Lc	-0.59	8.54	0.005
(3) Species recognition	No. <i>Anolis</i>	-9.13	0	0.323
(4) Sexual selection, natural selection and species recognition	SSD, TBF, no. <i>Anolis</i>	-9.09	0.04	0.316
(5) Sexual and natural selection	SSD, TBF	-3.10	6.03	0.016
(6) Natural selection and species recognition	TBF, no. <i>Anolis</i>	-8.15	0.98	0.197
(7) Sexual selection and species recognition	SSD, no. <i>Anolis</i>	-7.50	1.63	0.143

The model with the lowest Δ_i value and the highest w_i is considered the 'best' model among the candidate models (in bold). SSD, sexual size dimorphism; TBF, tail break frequency; Lc, absence/presence *Leiocephalus carinatus* lizards.

thesis (i.e. model with the absence/presence of *L. carinatus*, island area and tail break frequency as covariates). It has an 87% chance of being the best model among those considered in the set of candidate models. None of the other six models have substantial empirical support (all $\Delta_i > 4.58$, Table 3). On islands where *A. sagrei* co-occurs with *L. carinatus* lizards, females have larger relative dewlaps than on islands without (Fig. 4a). Residual dewlap size is smaller, however, on larger islands and on islands with a higher incidence of tail autotomy (Figs 4b,c).

Dewlap pattern in females

Tail break frequency appears to be the most important predictor variable when comparing the summed Akaike weights ($w_+ = 0.57$) of the three covariates in the natural selection model. The absence/presence of *L. carinatus* lizards ($w_+ = 0.31$) and island area ($w_+ = 0.52$) are less important predictor variables. We, therefore, included only tail break frequency as natural selection-related covariate in the models combining natural selection and sexual selection and/or species recognition hypotheses.

In female *A. sagrei*, the model, with dewlap pattern as a dependent variable, including the number of *Anolis* species as a covariate has the lowest Δ_i value and highest w_i (Table 3). It has a 32% chance of being the best model among the seven candidate models. The dewlap pattern in females is more complex when more *Anolis* species co-occur (Fig. 3b). Still, the models based the species recognition and natural selection hypotheses, the species recognition and sexual selection hypotheses, and all three hypotheses also have considerable

empirical support ($\Delta_i < 2$, Table 3). Summing the Akaike weights of the different covariates included in these models shows that the number of congeneric species is the most important predictor variable ($w_+ = 0.98$), followed by tail break frequency ($w_+ = 0.53$). Sexual size dimorphism is the least important predictor variable ($w_+ = 0.48$).

Comparison of dewlap pattern frequency distributions

As the number of co-occurring *Anolis* species seems to be one of the most important factors explaining the variation in dewlap pattern in both male and female *A. sagrei*, we subsequently performed Kruskal–Wallis tests and compared the frequency distributions of individual dewlap pattern among the different sympatric species. The frequency distributions with regard to dewlap pattern differ significantly in both males and females of the four sympatric species (*A. sagrei*, *A. carolinensis*, *A. distichus* and *A. angusticeps*) on four-species islands ($\chi^2_3 = 134.73$, $P < 0.0001$; $\chi^2_3 = 93.5$, $P < 0.0001$ respectively), among males and females of *A. sagrei*, *A. carolinensis* and *A. distichus* on three-species islands ($\chi^2_2 = 14.29$, $P = 0.001$; $\chi^2_2 = 22.07$, $P < 0.0001$ respectively) and among males and females of *A. sagrei* and *A. carolinensis* on two-species islands ($\chi^2_1 = 25.76$, $P < 0.0001$; $\chi^2_1 = 4.17$, $P = 0.04$ respectively). The frequency distribution of dewlap patterning in *A. sagrei* shows an obvious shift to more complex dewlaps (i.e. left on Fig. 5) when comparing two-, three- and four-species islands. In addition, the proportion of *A. sagrei* individuals with solid dewlaps decreases from two-species, over three-species islands to four-species islands (Fig. 5).

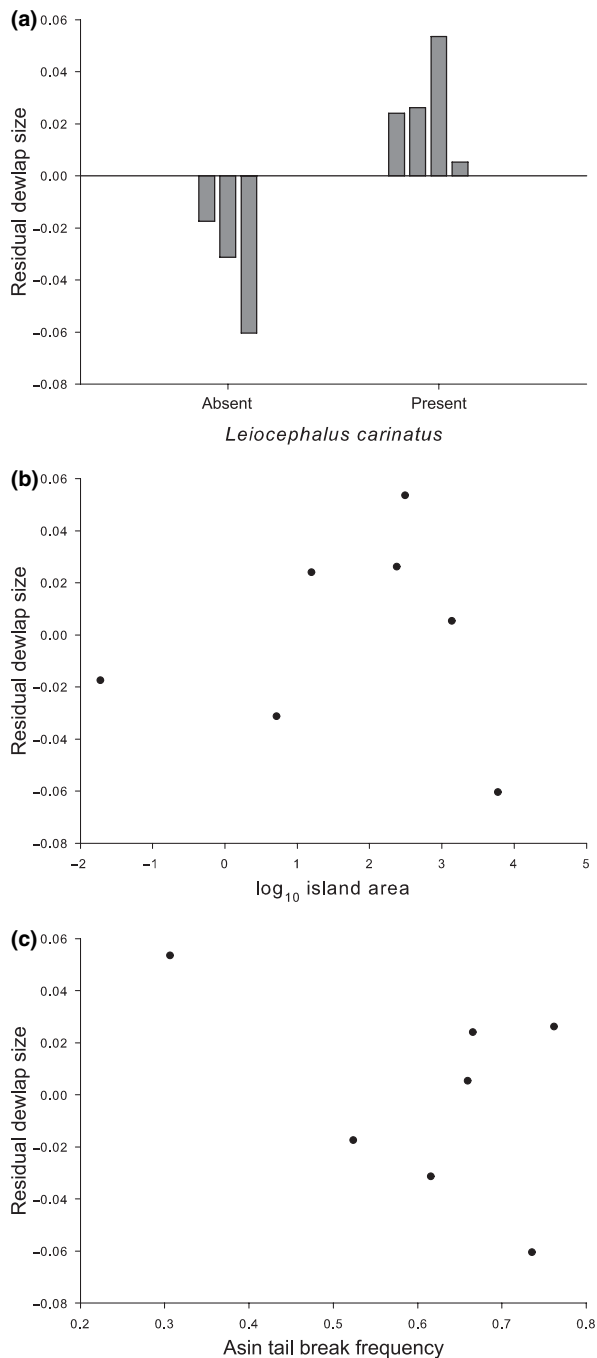


Fig. 4 Plot of female residual dewlap size in seven *A. sagrei* populations from the Bahamas against the covariates in the model with the lowest Δ_i and highest w_i of all alternative models: (a) absence or presence of *Leiocephalus carinatus* lizards ($w_+ = 0.99$), (b) island area (\log_{10} transformed; $w_+ = 0.98$) and (c) tail break frequency (arcsine transformed; $w_+ = 0.98$). Female residual dewlap size is larger on islands with *L. carinatus* lizards present, whereas it is smaller on larger islands with higher levels of predation pressure. Female residual dewlap size thus represents an evolutionary balance between opposing natural selection pressures.

Discussion

Evolution of dewlaps in *A. sagrei*

Our results suggest that two different aspects (i.e. size and pattern) of the same morphological structure (i.e. the dewlap) are susceptible to different selective pressures. Whereas the diversity in dewlap size seems to be primarily explained by natural selection and to some extent by sexual selection, dewlap pattern seems to play a major role in species recognition. Also, dewlap size and pattern complexity do not appear to co-evolve as they are not significantly correlated. That multiple signals may serve divergent roles has been demonstrated previously. For instance, different structures (e.g. song vs. plumage diversity in finches, Badyaev *et al.*, 2002; belly vs. throat patches in *Urosaurus ornatus* lizards, Meyers *et al.*, 2006) may convey different kinds of information (e.g. behavioural aggression vs. dominance; Meyers *et al.*, 2006), and/or different aspects of the same structure (e.g. badge colour and size) may undergo divergent sexual selection pressures (e.g. intra- vs. intersexual selection; Andersson *et al.*, 2002; Pryke *et al.*, 2002). However, two closely related features of the same structure serving two divergent functions, and undergoing different kinds of selective pressures (i.e. natural and/or sexual selection vs. species recognition) as has been shown here is unusual.

Evolution of dewlap pattern

Dewlap pattern seems to vary primarily as a function of the number of sympatric *Anolis* species in both males and females. Not only does the complexity of the pattern change, it changes in relation to the dewlap pattern of the co-existing *Anolis* species. Although, we do not have data on dewlap characteristics of *A. sagrei* occurring in absence of congeneric species, these results at least suggest character displacement occurs with respect to dewlap pattern. Possessing distinctively patterned, unique dewlaps when co-occurring with congeneric species may thus facilitate rapid and unambiguous identification of a conspecific (Rand & Williams, 1970; Figuerola & Green, 2000; Seddon, 2005; Ord & Martins, 2006). Although it has been shown experimentally that at least some *Anolis* species are able to discern conspecifics from heterospecifics based on the display behaviour and dewlap colour (Losos, 1985; Macedonia & Stamps, 1994; Macedonia *et al.*, 1994), Nicholson *et al.* (2007) only found weak evidence in support of the species recognition hypothesis when comparing dewlap patterns across *Anolis* species. In Nicholson's comparative analysis, sympatrically occurring *Anolis* species differ significantly in dewlap configuration in three of four communities. Because of the great diversity in dewlap morphologies, however, they concluded that species from one community may differ in dewlap pattern by chance alone

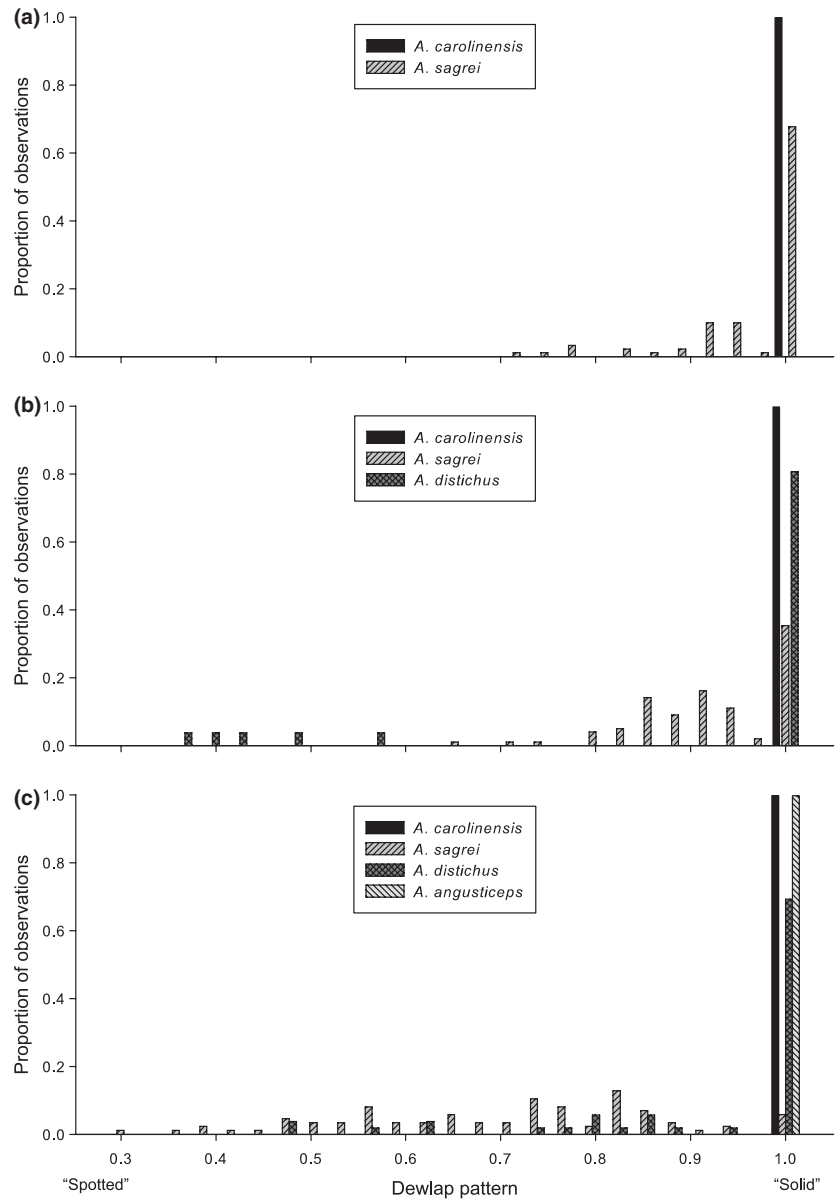


Fig. 5 Frequency distribution, shown as the proportion of observations, of dewlap patterning of sympatrically occurring *Anolis* lizards on (a) two-species islands, (b) three-species islands and (c) four-species islands. Sympatrically occurring species differ with respect to dewlap pattern. The proportion of *Anolis sagrei* individuals with complex dewlap patterns (i.e. basal and striped) increases with the number of sympatric congeneric species, whereas the proportion of *A. sagrei* individuals with solid dewlaps decreases. Observations on males and females are combined. Bar colours and patterns represent different species.

(Nicholson *et al.*, 2007). Although we cannot rule out this possibility in our system, it seems rather unlikely that these complex patterns arose by chance alone, as the most complex dewlaps only occurred on islands with four sympatric *Anolis* species. This argument is further supported by the observation that this pattern holds for both males and females. In light of the species recognition hypothesis, this is not surprising as avoiding costly mating errors may be advantageous for both sexes.

Evolution of dewlap size

Contrary to dewlap pattern, relative dewlap size does not seem to serve a prominent role in species recognition but

seems to be subjected to a different set of natural and sexual selective pressures. In addition, selective pressures on relative dewlap size seem to differ for males and females. Whereas male dewlap size is under natural selection and sexual selection to some extent, natural selection is the main force driving the evolution of dewlap size in females. Male *A. sagrei* have relatively larger dewlaps when sexual selection, as estimated by the degree of sexual size dimorphism, is stronger. Possibly, dewlap size is determined by intrasexual selection (i.e. male–male competition), as in territorial *Anolis* lizards it acts as an honest signal of bite force and fighting ability (Vanhooydonck *et al.*, 2005a, b; Lailvaux & Irschick, 2007), whereas its role during intersexual interactions

(i.e. female choice) is unclear (Lailvaux & Irschick, 2006). We realize two recent studies (Tokarz *et al.*, 2003; Lailvaux & Irschick, 2007) on the functional role of the dewlap in male *A. sagrei* that do not corroborate this idea. However, in the first (Tokarz *et al.*, 2003), only males with established territories were used and if dewlap size is important in settling territorial fights, its functional role may be more prominent in young males without established territories. A positive correlation between dewlap size and bite force in small mature males but not large mature males of another *Anolis* species, *A. carolinensis*, corroborates this idea (Vanhooydonck *et al.*, 2005a). In the second (Lailvaux & Irschick, 2007), data for an *A. sagrei* population from the largest, one of the most diverse, Caribbean islands (i.e. Cuba), were combined with data for a population from one of the smaller Bahamian islands, i.e. South Bimini. Thus, the lack of an association between dewlap size and intensity of sexual selection in the study by Lailvaux & Irschick (2007) potentially represents a sampling artefact.

The natural selection hypothesis posits that large, conspicuous sexual signals render the bearer more susceptible to predation (Endler, 1992; Andersson, 1994; Zuk & Kolluru, 1998). Our results, however, do not corroborate this idea as both male and female *A. sagrei* occurring in sympatry with predatory *Leiocephalus* lizards have larger relative dewlaps than *A. sagrei* from islands without. We believe that the association between *Leiocephalus* lizards and dewlap size in both male and female *A. sagrei* may be explained by the pursuit deterrence hypothesis. The pursuit deterrence hypothesis is somewhat controversial but examples of pursuit deterrent signals have been described for a number of taxa (review in Caro, 1995; Cooper, 2000). In general, pursuit deterrent displays signal to a predator that it has been detected, which causes the predator to give up its attempt to attack the prey (Caro, 1995). In *A. sagrei*, the dewlap may function as a pursuit deterrent signal during agonistic encounters with *Leiocephalus* lizards as some *Anolis* lizards are known to show extensive display behaviour, including extensions of the dewlap, when confronted with a predator. Even more so, this behaviour seems effective as snake predators have been observed to stop approaching *Anolis* lizards that start displaying (Leal & Rodriguez-Robles, 1995, 1997; Leal, 1999). In addition, the intensity of display appears to be correlated to locomotor capacity in *A. cristatellus* and can thus be interpreted as signalling the ability to escape a predatory attack (Leal, 1999). As dewlap size may indicate bite force and fighting ability (see also above), and anoles are known to bite and struggle when captured by predators (Leal & Rodriguez-Robles, 1995), dewlap size may also have evolved to warn predators that anoles have powerful bites and thus deter them from attacking. To corroborate this idea, however, we need observations on display and dewlap behaviour in *A. sagrei* when confronted with *Leiocephalus* lizards.

Whereas in males, selective pressures resulting from sexual selection and the presence of *Leiocephalus* lizards thus seem to override the constraining effect of natural selection pressures, this is not true in females. Although the presence of *L. carinatus* lizards is the predictor variable with the highest relative importance (i.e. $w_+ = 0.99$), island area and tail break frequency are only slightly less important (both $w_+ = 0.98$). Contrary to the effect of the presence of *L. carinatus* lizards on relative dewlap size in female *A. sagrei*, an increase in the tail break frequency and greater island size are associated with a decrease in the dewlap size in female *A. sagrei*, suggesting that natural selection does constrain dewlap size to some degree in female *A. sagrei*. This finding is in agreement with the natural selection hypothesis that posits that, in high predation environments, conspicuous signals are selected against because they draw the attention of predators (Endler, 1992; Andersson, 1994; Zuk & Kolluru, 1998). Instead of having the opposite effect from sexual selection pressures, the trade-off between the strength of predation pressure and the occurrence of predatory *Leiocephalus* lizards seems to drive the evolution of female dewlap size in *A. sagrei*. Female dewlap size thus seems to represent a balance between selective pressures on it being an effective pursuit deterrent signal to *Leiocephalus* lizards and being cryptic to other predators at the same time.

Alternative hypotheses

An alternative, nonmutually exclusive, hypothesis put forward to explain signal diversity among closely related species is the sensory drive hypothesis (cf. Endler & Théry, 1996; Endler & Basolo, 1998; Boughman, 2002; Leal & Fleishman, 2002, 2004). The sensory drive hypothesis assumes that natural selection acts on signals to be effective under their respective habitat conditions. More specifically, in *Anolis* lizards, it has been shown that dewlap colouration (i.e. spectral reflectance and transmittance) differs among species and populations occupying habitats with different light intensity and spectral quality (Leal & Fleishman, 2002, 2004). At the moment, we are unable to examine whether and how habitat light conditions influence the variation in dewlap size and pattern in Bahamian *A. sagrei*. Although, at first sight, *A. sagrei* seems to occur in similar environmental conditions (i.e. tropical, moist, densely vegetated habitats) on the seven islands under study here, we need spectrophotometric data of both the dewlap and habitat to explicitly test the importance of the sensory drive hypothesis in explaining the diversity in dewlap design in *A. sagrei*.

Conclusions

Our results suggest that two different aspects (i.e. size and pattern) of the same trait (i.e. dewlap) serve different roles and undergo differential selection pressures in *A. sagrei*.

lizards from the Bahamas. In addition, selective pressures acting on dewlap size and pattern vary independently and extensively among islands and populations, causing significant intraspecific diversity in the overall dewlap design. At this point, it remains unclear whether this result is specific for Bahamian *A. sagrei* or whether it can be generalized across all *Anolis* species. It seems plausible to expect though that similar processes underlie the extreme interspecific variation in anoline dewlap design.

In addition to interpopulation differences, selective pressures acting on dewlap design also differ for male and female *A. sagrei* lizards. Whereas male *A. sagrei* have larger relative dewlaps on islands where sexual selection pressure is greater and natural selection by predatory *Leiocephalus* lizards is high, relative dewlap size in females represents an evolutionary balance between the presence of *Leiocephalus* lizards and the presence of other agents of natural selection.

Acknowledgments

We would like to thank Andrew Hendry for statistical advice. This work was supported by an NSF grant to DJI (IOB 0421917). BV is a post-doctoral fellow of the Flemish Science Foundation (FWO-VI).

References

- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton.
- Andersson, S., Pryke, S.R., Örnberg, J., Lawes, M.J. & Andersson, M. 2002. Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signaling in a widowbird. *Am. Nat.* **160**: 683–691.
- Badyaev, A.V., Hill, G.E. & Weckworth, B.V. 2002. Species divergence in sexually selected traits: increase in song elaboration is related to decrease in plumage ornamentation in finches. *Evolution* **56**: 412–419.
- Bajema, C.J. 1984. *Evolution by Sexual Selection Theory Prior to 1900*. Van Nostrand Reinhold Co., New York.
- Bels, V. 1990. The mechanism of dewlap extension in *Anolis carolinensis* (Reptilia: Iguanidae) with histological analysis of the hyoid apparatus. *J. Morphol.* **206**: 225–244.
- Blanco, G. & De La Puente, J. 2002. Multiple elements of the black-billed magpie's tail correlate with variable honest information on quality in different age/sex classes. *Anim. Behav.* **63**: 217–225.
- Blondel, J., Perret, P., Anstett, M.-C. & Thébaud, C. 2002. Evolution of sexual size dimorphism in birds: test of hypotheses using blue tits in contrasted Mediterranean habitats. *J. Evol. Biol.* **15**: 440–450.
- Boughman, J.W. 2002. How sensory drive can promote speciation. *TREE* **17**: 571–577.
- Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Burnham, K.P. & Anderson, D.R. 2004. Multimodel inference. Understanding AIC and BIC in model selection. *Sociol. Methods Res.* **33**: 261–304.
- Butcher, G.S. & Rohwer, S. 1989. The evolution of conspicuous and distinctive coloration for communication in birds. *Curr. Ornithol.* **6**: 51–107.
- Butler, M.A., Schoener, T.W. & Losos, J.B. 2000. The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution* **54**: 259–272.
- Caro, T.M. 1995. Pursuit-deterrence revisited. *Trends Ecol. Evol.* **10**: 500–503.
- Cooper, W.E. Jr 2000. Pursuit deterrence in lizards. *Saudi. J. Biol. Sci.* **7**: 15–29.
- Echelle, A.F., Echelle, A.A. & Fitch, H.S. 1978. Inter- and intraspecific allometry in a display organ: the dewlap of *Anolis* (Iguanidae) species. *Copeia* **1978**: 245–250.
- Endler, J.A. 1983. Natural and sexual selection on color patterns in poeciliid fishes. *Environ. Biol. Fishes* **9**: 173–190.
- Endler, J.A. 1992. Signals, signal conditions, and the direction of evolution. *Am. Nat.* **139**: S125–S153.
- Endler, J.A. & Basolo, A.L. 1998. Sensory ecology, receiver biases, and sexual selection. *TREE* **13**: 415–420.
- Endler, J.A. & Théry, M. 1996. Interacting effects of lek placement, display behaviour, ambient light, and color patterns in three Neotropical forest-dwelling birds. *Am. Nat.* **148**: 421–452.
- Figuerola, J. & Green, A.J. 2000. The evolution of sexual dimorphism in relation to mating patterns, cavity nesting, insularity and sympatry in the Anseriformes. *Funct. Ecol.* **14**: 701–710.
- Fitch, H.S. & Hillis, D.M. 1984. The *Anolis* dewlap: interspecific variability and morphological associations with habitat. *Copeia* **1984**: 315–325.
- Foster, S.A. 1999. The geography of behaviour: an evolutionary perspective. *Trends Ecol. Evol.* **14**: 190–195.
- Foster, S.A., Scott, R.J. & Cresko, W.A. 1998. Nested biological variation and speciation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **353**: 207–218.
- Fox, S.F., Perea-Fox, S. & Franco, R.C. 1994. Development of the tail autotomy adaptation in lizards under disparate levels of predation at high and low elevations in Mexico. *Southwest. Nat.* **39**: 311–322.
- Grant, P.R. 1998. *Evolution on Islands*. Oxford University Press, Oxford.
- Greenberg, B. & Noble, G.K. 1944. Social behavior of the American chameleon (*Anolis carolinensis* Voigt). *Phys. Zool.* **17**: 392–439.
- Hamon, T.R. & Foote, C.J. 2005. Concurrent natural and sexual selection in wild male sockeye salmon, *Oncorhynchus nerka*. *Evolution* **59**: 1104–1118.
- Jaksic, F.M. & Greene, E.R. 1984. Correlates of tail losses in twelve species of *Liolaemus* lizards. *J. Herpetol.* **14**: 137–141.
- Jenssen, T.A., Orrell, K.S. & Lovern, M.B. 2000. Sexual dimorphisms in aggressive signal structure and use by a polygynous lizard, *Anolis carolinensis*. *Copeia* **2000**: 140–149.
- Kwiatkowski, M.A. 2003. Variation in conspicuousness among populations of an Iguanid lizard, *Sauromalus obesus* (=ater). *Copeia* **2003**: 481–492.
- Lailvaux, S.P. & Irschick, D.J. 2006. No evidence for female association with high-performance males in the green anole lizard, *Anolis carolinensis*. *Ethology* **112**: 707–715.
- Lailvaux, S.P. & Irschick, D.J. 2007. The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. *Am. Nat.* **170**: 573–586.

- Leal, M. 1999. Honest signalling during predator-prey interactions in the lizard *Anolis cristatellus*. *Anim. Behav.* **58**: 521–526.
- Leal, M. & Fleishman, L.J. 2002. Evidence for habitat partitioning based on adaptation to environmental light in a pair of sympatric lizard species. *Proc. R. Soc. Lond. B Biol. Sci.* **269**: 351–359.
- Leal, M. & Fleishman, L.J. 2004. Differences in visual signal design and detectability between allopatric populations of *Anolis* lizards. *Am. Nat.* **163**: 26–39.
- Leal, M. & Rodriguez-Robles, J.A. 1995. Antipredator responses of *Anolis cristatellus* (Sauria: Polychrotidae). *Copeia* **1995**: 155–161.
- Leal, M. & Rodriguez-Robles, J.A. 1997. Signalling displays during predator-prey interactions in a Puerto Rican anole, *Anolis cristatellus*. *Anim. Behav.* **54**: 1147–1154.
- Lewkiewicz, D.A. & Zuk, M. 2004. Latency to resume calling after disturbance in the field cricket, *Teleogryllus oceanicus*, corresponds to population-level differences in parasitism risk. *Behav. Ecol. Sociobiol.* **55**: 569–573.
- Losos, J.B. 1985. An experimental demonstration of the species-recognition role of *Anolis* dewlap color. *Copeia* **1985**: 905–910.
- Losos, J.B. & Chu, L. 1998. Examination of factors potentially affecting dewlap size in Caribbean anoles. *Copeia* **1998**: 430–438.
- Losos, J.B. & Schluter, D. 2000. Analysis of an evolutionary species-area relationship. *Nature* **408**: 847–850.
- Losos, J.B., Irschick, D.J. & Schoener, T.W. 1994. Adaptation and constraint in the evolution of specialization of Bahamian *Anolis* lizards. *Evolution* **48**: 1786–1798.
- Losos, J.B., Butler, M. & Schoener, T.W. 2003. Sexual dimorphism in body size and shape in relation to habitat use among species of Caribbean *Anolis* lizards. In: *Lizard Social Behavior* (S.F. Fox, J.K. McCoy & T.A. Baird, eds), pp. 356–380. Johns Hopkins University Press, Baltimore, MD.
- Lovern, M.B. & Jenssen, T.A. 2001. The effects of context, sex, and body size on staged social interactions in juvenile male and female green anoles (*Anolis carolinensis*). *Behaviour* **138**: 1117–1135.
- MacArthur, R.H. & Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- Macedonia, J.M. & Stamps, J.A. 1994. Species recognition in *Anolis grahami* (Sauria: Iguanidae): evidence from responses to video playbacks of conspecific and heterospecific displays. *Ethology* **98**: 246–264.
- Macedonia, J.M., Evans, C.S. & Losos, J.B. 1994. Male *Anolis* lizards discriminate video-recorded conspecific and heterospecific displays. *Anim. Behav.* **47**: 1220–1223.
- Macedonia, J.M., Brandt, Y. & Clark, D.L. 2002. Sexual dichromatism and differential conspicuousness in two populations of the common collared lizard (*Crotaphytus collaris*) from Utah and New Mexico, USA. *Biol. J. Linn. Soc.* **77**: 67–85.
- McLaughlin, J.F. & Roughgarden, J. 1989. Avian predation on *Anolis* lizards in the Northeastern Caribbean: an inter-island contrast. *Ecology* **70**: 617–628.
- Meyers, J.J., Irschick, D.J., Vanhooydonck, B. & Herrel, A. 2006. Divergent roles for multiple signals in a polygynous lizard. *Funct. Ecol.* **20**: 709–716.
- Millar, N.P., Reznick, D.N., Kinnison, M.T. & Hendry, A.P. 2006. Disentangling the selective factors that act on male colour in wild guppies. *Oikos* **113**: 1–12.
- Moyaho, A., Garcia, C.M. & Manjarrez, J. 2004. Predation risk is associated with the geographic variation of a sexually selected trait in a viviparous fish (*Xenotoca variata*). *J. Zool. Lond.* **262**: 265–270.
- Nicholson, K.E., Harmon, L.J. & Losos, J.B. 2007. Evolution of *Anolis* lizard dewlap diversity. *PLoS ONE* **2**: e274.
- Ord, T.J. & Martins, E.P. 2006. Tracing the origins of signal diversity in anole lizards: phylogenetic approaches to inferring the evolution of complex behaviour. *Anim. Behav.* **71**: 1411–1429.
- Orrell, K.A. & Jenssen, T.A. 2003. Heterosexual signalling by the lizard *Anolis carolinensis*, with intersexual comparisons across contexts. *Behaviour* **140**: 603–634.
- Pough, F.H., Andrews, R.M., Cadle, J.E., Savitsky, A.H. & Wells, K.D. 2001. *Herpetology*. Prentice Hall, Upper Saddle River, NJ.
- Price, T. 1998. Sexual selection and natural selection in bird speciation. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **353**: 251–260.
- Pryke, S.R., Andersson, S., Lawes, M.J. & Piper, S.E. 2002. Carotenoid status signaling in captive and wild red-collared widowbirds: independent effects of badge size and color. *Behav. Ecol.* **13**: 622–631.
- Rand, A.S. & Williams, E.E. 1970. An estimation of redundancy and information content of anole dewlaps. *Am. Nat.* **104**: 99–103.
- Ricklefs, R.E. & Bermingham, E. 2004. History and the species-area relationship in Lesser Antillean birds. *Am. Nat.* **163**: 227–239.
- Schoener, T.W. & Schoener, A. 1978. Inverse relation of survival of lizards with island size and avifaunal richness. *Nature* **274**: 685–687.
- Schoener, T.W. & Schoener, A. 1980. Ecological and demographic correlates of injury rates in some Bahamian *Anolis* lizards. *Copeia* **1980**: 839–850.
- Schoener, T.W. & Schoener, A. 1982. The ecological correlates of survival in some Bahamian *Anolis* lizards. *Oikos* **39**: 1–16.
- Schoener, T.W., Slade, J.B. & Stinson, C.H. 1982. Diet and sexual dimorphism in the very catholic lizard genus, *Leiocephalus* of the Bahamas. *Oecologia* **53**: 160–169.
- Schoener, T.W., Spiller, D.A. & Losos, J.B. 2002. Predation on a common *Anolis* lizard: can the food-web effects of a devastating predator be reversed? *Ecol. Monogr.* **72**: 383–407.
- Schwartz, A. & Henderson, R.W. 1991. *Amphibians and Reptiles of the West Indies*. University of Florida Press, Gainesville, FL.
- Seddon, N. 2005. Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution* **59**: 200–215.
- Sokal, R.R. & Rohlf, F.J. 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*. W. H. Freeman & Co., New York.
- Stuart-Fox, D.M. & Ord, T.J. 2004. Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proc. R. Soc. Lond. B Biol. Sci.* **271**: 2249–2255.
- Stuart-Fox, D.M., Moussalli, A., Johnston, G.R. & Owens, I.P.F. 2004. Evolution of color variation in dragon lizards: quantitative tests of the role of crypsis and local adaptation. *Evolution* **58**: 1549–1559.
- Stuessy, T.F. & Ono, M. 1998. *Evolution and Speciation of Island Plants*. Cambridge University Press, Cambridge.
- Svensson, E.I., Eroukhmanoff, F. & Friberg, M. 2006. Effects of natural and sexual selection in adaptive population divergence and premating isolation in a damselfly. *Evolution* **60**: 1242–1253.

- Tokarz, R.R., Paterson, A.V. & McMann, S. 2003. Laboratory and field test of the functional significance of the male's dewlap in the lizard *Anolis sagrei*. *Copeia* **2003**: 502–511.
- Turner, F.B., Medica, P.A., Jennrich, R.I. & Maza, B.G. 1982. Frequencies of broken tails among *Uta stansburiana* in Southern Nevada and a test of the predation hypothesis. *Copeia* **1982**: 835–840.
- Vanhooydonck, B., Herrel, A., Van Damme, R., Meyers, J.J. & Irschick, D.J. 2005a. The relationship between dewlap size and performance changes with age and sex in a green anole (*Anolis carolinensis*) lizard population. *Behav. Ecol. Sociobiol.* **59**: 157–165.
- Vanhooydonck, B., Herrel, A., Van Damme, R. & Irschick, D.J. 2005b. Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? *Funct. Ecol.* **19**: 38–42.
- Williams, E.E. & Rand, A.S. 1977. Species recognition, dewlap function and faunal size. *Am. Zool.* **17**: 261–270.
- Zuk, M. & Kolluru, G.R. 1998. Exploitation of sexual signals by predators and parasitoids. *Q. Rev. Biol.* **73**: 415–438.

Received 3 March 2008; revised 5 September 2008; accepted 26 September 2008