

Examination of Factors Potentially Affecting Dewlap Size in Caribbean Anoles

JONATHAN B. LOSOS AND LING-RU CHU

The dewlaps of anoles vary greatly in size, including some species that have no dewlap at all. The dewlap serves many purposes—including courtship, territorial interactions, species recognition, and predator deterrence—and must be an effective communicatory signal in different light environments. We measured dewlap size in 52 species of Caribbean anoles to test a variety of hypotheses concerning the evolution of dewlap size. Species with conspicuous body coloration or patterning tend to have relatively smaller dewlaps than do other species. In addition, the data suggest the possibility that species in poorly lit habitats may have relatively larger dewlaps than species in brighter habitats. By contrast, no relationship exists between relative dewlap size and structural habitat, display rate, or sexual size dimorphism. Further, comparisons of the dewlaps of sympatric species do not support the hypothesis that differences in dewlap size aid in species recognition.

ONE of the defining characteristics of anoline lizards and their close relatives is possession of an extensible throat fan, termed a dewlap. Anoles display a remarkable diversity in dewlap configuration, including species with dewlaps spanning the spectrum from red to blue, as well as purple, and even ultraviolet (Fleishman et al., 1993); species with dewlap stripes, spots, splotches, and multiple colors; species with extremely large dewlaps; and species with no dewlap at all [see illustrations in Schwartz and Henderson (1985)]. This diversity may result from the many functions of the dewlap, which is used in courtship, intrasexual interactions, species recognition, and predator deterrence (Williams and Rand, 1977; Jenssen, 1978; Leal and Rodríguez-Robles, 1997).

Three hypotheses have been proposed to explain anole dewlap diversity. In the species recognition hypothesis, Rand and Williams (1970) noted that, at La Palma, Dominican Republic, each of eight sympatric anoles could be identified by its unique combination of dewlap variables (i.e., color, size, and patterning; hereafter referred to as “dewlap configuration”). Consequently, they argued that anole dewlap diversity evolved as a means of species recognition, which could be important both in territorial and courtship interactions. In the sexual selection hypothesis, Fitch and Hillis (1984) found, in a sample of 38 Central American anole taxa, that males of species living in seasonal habitats had larger dewlaps than did species living in aseasonal habitats. They hypothesized that shorter breeding seasons in the seasonal habitats resulted in more intense competition for mates, in turn resulting in selection for more exaggerated signalling capability. In support of this explanation, Fitch and Hillis (1984) found a correlation between sexual size dimorphism,

often considered to be a function of degree of sexual selection, and dewlap size. In the third hypothesis, communication effectiveness, the dewlap is used as a signal to communicate a message to another animal in all contexts. However, the effectiveness of a particular signal is affected by the environment in which it occurs (Endler, 1993). For example, in a poorly lit habitat, a light colored dewlap might be most effective, whereas in bright habitats, darker dewlaps may be more conspicuous (Fleishman, 1992).

Most research to date has focused on the importance of dewlap color. Distributional (Webster and Burns, 1973) and experimental (Losos, 1985; see also Macedonia and Stamps, 1994) studies both suggest that dewlap color plays an important role in species recognition, although color may be less important for species that normally occur in allopatry, such as *A. carolinensis* in Florida (Greenberg and Noble, 1944; Crews, 1975; but see Sigmund, 1983). Habitat illumination also affects dewlap color; yellow and white dewlaps are more common in forest-dwelling species, whereas red, brown, and blue are more frequent in species occurring in the open (Fleishman, 1992).

By contrast, little attention has been paid to other aspects of the dewlap. In this study, we examine hypotheses concerning differences in dewlap size among anoles. Dewlap size can vary substantially both among species at a given locality, as Rand and Williams (1970) noted, and among closely related species [e.g., *A. poncensis* has an extremely small dewlap, whereas its close relatives *A. krugi* and *A. pulchellus* have relatively large dewlaps (Williams and Rand, 1977; this study)]. Despite this interspecific variation in dewlap size, only Fitch and Hillis' (1984) study of Central American anoles has investigated factors affecting dewlap size, although Echelle et al. (1971) hypothesized an effect of habitat illumination.

We examined six factors that could potentially affect dewlap size: (1) sexual size dimorphism; (2) display rate; (3) species recognition; (4) habitat structure; (5) habitat illumination; and (6) body ornamentation. We investigated whether sexual size dimorphism and male dewlap size are related among Caribbean anoles, as they are among mainland anoles (Fitch and Hillis, 1984).

Given that anole species differ in social behavior, one might predict a relationship between frequency of display behavior and dewlap size. However, whether the relationship should be positive or negative is not clear. On one hand, species that display rarely might need particularly large dewlaps to maximize the effectiveness of their rare displays. Alternatively, displays might not be an important element of social structure in some species; such species might display rarely and also might have small dewlaps.

If dewlap size is important in species recognition, one might expect sympatric anoles to have dewlaps that are greatly different in size and thus easily distinguishable. We investigated whether sympatric anole species differ in dewlap size more than expected by chance.

On each island in the Greater Antilles, sympatric species differ in their structural habitat use. Independent evolutionary radiations on each of these islands (Williams, 1983; Burnell and Hedges, 1990; Jackman et al., in press) have produced the same set of habitat specialists, which are termed "ecomorphs" and named for the structural habitat they most frequently use [e.g., "trunk-ground," "grass-bush" (Williams, 1983)]. One might predict that the ecomorph classes would differ in dewlap size either as a direct consequence of differences in the structure of the habitat they use (e.g., cluttered structural habitats might make large dewlaps ineffective or prevent their use) or as a result of associated differences in behavior (Moermond, 1979, 1981; Losos, 1990) or social structure (Schoener and Schoener, 1982; Hicks and Trivers, 1983).

Larger dewlaps may be required for effective communication in dimly lit habitats. We investigated whether an inverse relationship exists between dewlap size and light levels within a species' habitat.

Dewlap size might be affected by whether a species possesses other means of signalling. In particular, Williams and Rand (1977) suggested that for signalling some species use ornamentation on the body, including both conspicuous colors and patterns, rather than the dewlap. We investigated whether species with conspicuous ornamentation have smaller dewlaps than species without such ornamentation.

MATERIALS AND METHODS

To analyze the importance of the six factors mentioned above, we measured the dewlap of 243 male anoles of 52 species. We included only males because females of most Caribbean anole species do not have dewlaps. Measurements were made by photographing the dewlap of an adult male lizard (usually anesthetized) lying on its side with its dewlap pulled out to maximal extent with a pair of forceps. Most photographs were taken with the same camera and lens at a constant focal distance; other photographs included objects of known dimensions for scaling. Dewlap area was measured from tracings taken from the slides using the Morphosys video-imaging system (Meacham and Duncan, 1990). Because dewlap patterning extends onto the throat skin of some species, we included this area and considered the bottom of the lower jaw as the top edge of the dewlap. To remove the effect of body size on dewlap area, we regressed area against snout-vent length (SVL), both \ln -transformed, for all individuals and used the residuals as a measure of relative dewlap size. We chose to use all individuals, rather than species' means, for the calculations of residuals because of the substantial variation in SVL within some of the species.

Sexual size dimorphism.—Measurements of sexual size dimorphism were based on the data used in Schoener (1969, 1970). The value of dimorphism for a species was calculated as male size/female size, both of which represented the mean SVL of the largest third of all specimens examined.

Display rate.—Rate of displaying (bobbing and/or dewlapping) for 21 species was calculated from focal animal samples lasting 5–20 min (Losos, 1990, unpubl. data). Two measures of display frequency were calculated: mean number of displays per minute and percentage of time spent displaying. Behavioral data were collected on at least 15 individuals for most species, and mean species values were used in analyses.

Species recognition.—We chose representative localities from each of the Greater Antilles to test the hypothesis that variation in dewlap size might be important for species recognition (Table 1). If dewlap size is a species-recognition signal, we might make two predictions. First, sympatric species should exhibit substantial differences in dewlap size. We examined this hypothesis by investigating whether the variance in dewlap size among sympatric species was unusually large relative to

TABLE 1. REPRESENTATIVE COMMUNITIES CONSIDERED IN THIS STUDY.

Locality	Soroa, Cuba ¹	La Palma, Hispaniola ²	Negril, Jamaica	Luquillo Mtns., Puerto Rico
Species*	allogus alutaceus ^a angusticeps ^a homolechis ^a loysiana ^a luteogularis mestrei porcatus ^a sagrei vermiculatus	aliniger ^b chlorocyanus ^c christopheii cybotes distichus etheridgei insolitus ^c semilineatus ^b	garmani grahami lineatopus ^d opalinus ^d valencienni	crystalinus ^f cuvieri evermanni ^e gundlachi ^e krugi ^e occultus pulchellus ^f stratulus
Variance in Actual dewlap size**	0.65	0.19	0.28	0.71
Variance in relative dewlap size***	0.62	0.24	0.09	0.03

¹ At least one species of *Chamaeleotis* also occurs at Soroa, but we have no data on adult males. *Anolis vermiculatus* was included in the variance in size analysis but was not included in the dewlap configuration analysis because it has no dewlap.

² We have no data for the crown-giant *A. ricordii*. Hence, the variance in absolute dewlap size is undoubtedly much greater than the figure reported here. For *A. cybotes*, we have data on dewlap configuration but not relative dewlap area. Hence, we substituted the value for relative dewlap area from the closely related *A. longitibialis*.

* Species with similar dewlap configurations (i.e., similar dewlap scale and color pattern) in the same locality are followed by the same letter.

** Variance in the relative size of the dewlap for the entire dataset is 0.89.

*** Variance in the relative size of the dewlap for the entire dataset is 0.40.

the variance in the sample as a whole. Second, Rand and Williams (1970) suggested that sympatric species with similar dewlap patterning (i.e., the color pattern, not the colors themselves) tended to differ in dewlap size. To test this hypothesis, we scored two aspects of dewlap patterning [modified from Rand and Williams (1970)]: color pattern on the skin of the dewlap and pattern of the scales on the dewlap. Anoles were considered to be similar in dewlap configuration if they had the same color and scale pattern. We considered three categories of dewlap patterning: uniform color throughout the dewlap, different colors on the margin and interior of the dewlap, and patches of color different from the color of the rest of the dewlap (note that these categories refer to the pattern of color, but not to the colors themselves; thus, species with dewlaps of different colors but the same pattern would be considered similar for the purposes of this analysis). The pattern of the scales on the dewlap was also divided into three categories: regular dispersion of scales over the dewlap, irregular dispersion, distinct lines separated by scaleless skin. We then asked whether, within a locality, species with the same dewlap configuration were more dissimilar in dewlap size than pairs of species with different configurations (in one instance, two species both had dewlaps with patches of different colors, but because the patches were arranged very differently in the two species, the dewlaps were considered to have different patterns). We used a randomization test to

examine this hypothesis by calculating the mean difference in dewlap size among all pairs of species with similar dewlap configurations and then comparing this value with the difference in all possible combinations of species at that locality; the randomization calculated what proportion of all possible combinations gave a larger value than the observed mean difference. Analyses considered both actual and relative dewlap size; the latter was calculated as the difference in residual dewlap area for the two species.

Habitat structure.—The effect of habitat structure on dewlap area was assessed by comparisons among the ecomorph classes. We investigated whether the six ecomorphs, which use different structural habitats, differ in relative dewlap size.

Habitat illumination.—Examining the effect of habitat illumination is more difficult because no quantitative data exist on habitat light levels. However, we were able to identify two pairs and three trios of closely related and ecologically similar species that clearly differ in habitat illumination (Appendix). For these 13 species, there were eight comparisons [two for each trio—dimmiest vs intermediate and intermediate vs brightest (the transitive property of inequalities sometimes renders the comparison of dimmiest vs brightest redundant with the previous two comparisons; thus this comparison is not included)—and one for each pair]. We

scored the number of comparisons in which the species living in the more poorly illuminated habitat has a larger relative dewlap size than the species in the better illuminated habitat.

Body ornamentation.—To examine whether an inverse relationship exists between body patterning and relative dewlap size, we identified a number of species (Appendix) with conspicuous body coloration and patterns (e.g., axillary patches). We then asked whether these species had larger dewlaps than the other species in our dataset. The definition of what constitutes conspicuous coloration and patterning is inherently arbitrary. We included all species suggested by Williams and Rand (1977) when they proposed the body ornamentation hypothesis and added several additional species. To be conservative, we excluded several species with small dewlaps (e.g., *A. allisoni*, *A. ophiolepis*) that might have been considered to have conspicuous ornamentation.

Statistical analyses.—Interspecific comparative analyses must be conducted in the context of the phylogenetic relationships of the taxa included (Felsenstein, 1985). We used a phylogeny for anoles based on mitochondrial DNA sequence data (Jackman et al., 1997, in press). In some cases, we had dewlap data on species not included in the phylogeny; however, the phylogenetic relationships of many of these species are known from other studies [e.g., *A. evermanni* is the sister taxon of *A. stratulus* (Williams, 1972; Gorman et al., 1983)]; consequently, these species were added to the phylogeny.

Analyses of the relationship between dewlap area, display rate, and sexual dimorphism were conducted using the method of independent contrasts (Felsenstein, 1985). These analyses were conducted twice using different models of evolutionary change. In the speciation model, we assigned all branches a length of one (Garland et al., 1992). In the gradual model, we calculated branch lengths from the DNA data using the Kitch option of PHYLIP (Felsenstein, 1985) assuming that DNA divergence conforms to a molecular clock (see Jackman et al., in press). For species added to the phylogeny (e.g., *A. evermanni*), we assumed that the time of divergence from its sister taxon occurred midway along the branch leading to the sister taxon's ancestral node. Regressions were calculated through the origin (Garland et al., 1992). We investigated whether branch lengths were appropriately standardized following Garland et al. (1992). In all gradual analyses, branch lengths were standardized by \ln -transformation following Garland et al. (1992); results using the

transformed branch lengths were qualitatively identical to those using nontransformed branch lengths. Transformations were not necessary in the speciation analyses.

For the examination of differences in dewlap area between the ecomorphs, a phylogenetic analysis of variance (ANOVA) is necessary (Garland et al., 1993). To conduct this analysis, we simulated character evolution along the phylogenetic tree, thus assigning values of relative dewlap area to each terminal taxon. We then calculated the F -statistic for this simulated dataset and repeated the analysis 1000 times, computing the number of times in which the simulated F -statistic exceeded that observed in the real dataset. We considered the results significant if fewer than 5% of the simulation trials yielded an F -statistic greater than that observed in the real dataset. The phylogenetic ANOVA was conducted twice, using the same two models of evolution as above. In the speciation evolution model, we assigned change in dewlap area for a branch of the tree by drawing once from a normal distribution with mean of zero. For the gradual model, the number of draws for a branch was proportional to the length of that branch as calculated above. In both analyses, the variance of the normal distribution was calibrated so as to produce a variance among the terminal "species" approximately the same as that observed in the real dataset (following Garland et al., 1993).

In a similar manner, we used phylogenetic simulation in the habitat illumination and body coloration analyses. In both cases, the simulations produced values for each species in the analysis; we then calculated the same statistic as we did with the real data. This procedure was repeated 1000 times, using both models of character evolution, to establish a test statistic distribution.

RESULTS

Dewlap area and SVL were strongly related both among all individuals ($r^2 = 0.49$) and among species means ($r^2 = 0.56$). However, substantial variation existed as well (Fig. 1).

Display rate and sexual size dimorphism.—No relationship existed between dewlap area and percentage of time spent displaying (gradual model, $r^2 = 0.06$, $F_{1,17} = 2.00$, $P = 0.18$; speciation model, $r^2 = 0.07$, $F_{1,17} = 1.26$, $P = 0.28$), displays per minute (gradual model, $r^2 = 0.03$, $F_{1,17} = 1.56$, $P = 0.23$; speciation model, $r^2 = 0.04$, $F_{1,17} = 0.72$, $P = 0.41$), or degree of sexual dimorphism (gradual model, $r^2 = 0.05$, $F_{1,37} =$

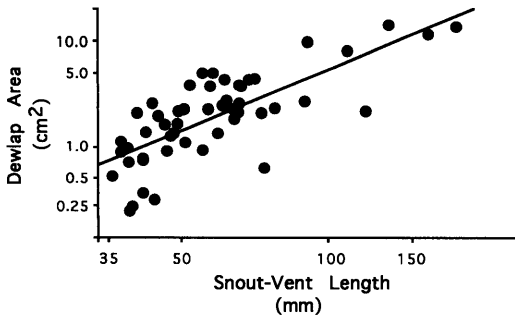


Fig. 1. Dewlap area versus snout-vent length. Each point is the mean value for a species. Size of the dewlap is nonzero even in species lacking a dewlap because part of the throat is included in the measurement of dewlap area. Note that, in statistical analyses, residuals were calculated using all individual points, rather than species' means.

1.78, $P = 0.19$; speciation model, $r^2 = 0.05$, $F_{1,37} = 1.8$, $P = 0.19$).

Species recognition.—Comparisons of the variance in absolute dewlap area reveal that none of the islands exhibits greater variance than the sample as a whole. This result is not surprising given that dewlap area and body size are correlated and that the distribution of body sizes within each of the islands and in the sample as a whole are approximately equivalent. Comparisons of the variance in relative dewlap area indicates that only the anoles of Cuba have a relatively large variance in relative dewlap area; all other localities exhibit smaller variance in relative dewlap area than does the dataset as a whole (Table 1). In Hispaniola, sympatric species with similar dewlap configurations tend to be dissimilar in relative dewlap size (Table 2). A similar pattern is suggested in Puerto Rico, but no such trend is apparent for Jamaica or Cuba. None of the localities provides evidence for a relationship between difference in absolute dewlap area and dewlap configuration (Table 2).

Habitat structure.—When phylogeny is not considered, variation exists in relative dewlap area among the ecomorph classes ($F_{5,34} = 2.75$, $P = 0.034$), primarily due to the large dewlaps of trunk-ground anoles (Fig. 2). However, closely related species are often similar in relative dewlap size (see data in the Appendix). For example, of the 10 trunk-ground anoles in the dataset, five are members of the *A. sagrei* group, four of which have extremely large dewlaps for their size (Appendix). When the analysis of variance is conducted within the context of the phylogenetic relationships, the observed F -value for the real data

TABLE 2. DIFFERENCES IN DEWLAP SIZE AMONG SYMPATRIC SPECIES.

	Cuba	Hispaniola	Jamaica	Puerto Rico
Relative dewlap size				
Mean difference in dewlap size of species with similar dewlap configurations	0.68	0.96	0.24	0.28
Mean difference in dewlap size between all species	0.71	0.55	0.37	0.20
Probability	0.66	0.067	0.80	0.19
Absolute dewlap size				
Mean difference in dewlap size of species with similar dewlap configurations	0.77	0.18	0.65	0.57
Mean difference in dewlap size between all species	0.88	0.67	0.63	0.87
Probability	0.61	0.99	0.40	0.79

is not particularly large. In the gradual analyses, 183 of the 1000 simulations produced F -values greater than in the observed dataset, whereas in the speciation simulations, 192 of the simulations exceeded the observed value.

Habitat illumination.—In the habitat illumination analysis, two of the three species trios were in perfect rank order with the species in the dimmest habitat having the largest dewlap and the species in the brightest habitat having the smallest. In the third trio, the brightest habitat species (*A. cooki*) has a larger dewlap than does the intermediate species (*A. cristatellus*), but both have smaller dewlaps than does *A. gundla-*

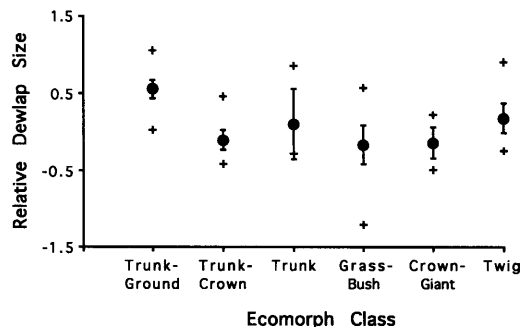


Fig. 2. Variation in relative dewlap size among ecomorph classes. Bars are standard errors; crosses indicate the largest and smallest value for each ecomorph class.

chi, which occurs in the forest interior. In the two species pairs, one pair was in the predicted order, and the other pair was in the opposite order. Thus, of eight comparisons, six were in the predicted direction. In the simulations, six or more comparisons were in this order in 12.2% of the simulations using a gradual model of evolution and 10.9% of the simulations using a speciation model.

Body ornamentation.—Both species without dewlaps (the closely related *A. bartschi* and *A. vermiculatus*) and three of the species with the smallest dewlaps (*A. aliniger*, *A. bahorucoensis*, and *A. poncensis*) have conspicuous body coloration or patterning. The nonphylogenetic analysis indicated that the 45 species without such coloration or patterning have relatively larger dewlaps than do the seven conspicuously ornamented species ($F_{1,47} = 11.24$, $P = 0.002$). In the simulations, only 0.6% of the gradual trials and 3.8% of the speciation trials provided an *F*-statistic as high or higher than the *F*-statistic value obtained in the nonphylogenetic analysis.

DISCUSSION

Many factors may have played a role in the evolution of anole dewlaps. For example, the dewlap may need to be able to convey information in a variety of different contexts, including interactions with conspecifics, heterospecific congeners, and predators. Evolution of the dewlap might be affected by the extent to which a species signals other individuals (both conspecific and heterospecific), the availability of alternative means of signalling, and the visual environment in which signalling usually occurs.

Despite all of these factors potentially impinging on dewlap evolution, we only found one factor significantly related to dewlap size: species with conspicuous body coloration or patterning tend to have smaller dewlaps than do species without such ornamentation. Williams and Rand (1977) suggested this hypothesis, arguing that these species may use their ornamentation as a signalling device in place of the dewlap. For example, Fitch and Henderson (1987) studied *A. bahorucoensis*, which has a small dewlap and bold body coloration and which appears to be heavily preyed upon by other anoles. They suggested that, although a dewlap can be seen at great distances, and thus may attract predators as well as conspecifics, the bold coloration of this species may be useful at close range for intraspecific communication but cryptic at greater distances. Detailed laboratory and field behavioral studies are now needed to assess whether

these species do, indeed, use their body ornamentation as a signal. In addition, an interesting comparison might be made between the species included in this analysis and several conspicuously colored or patterned species in the Lesser Antilles, which have moderately developed dewlaps (*A. marmoratus*, *A. ocellatus*, and *A. roquet*). Each of these species is not sympatric with any other anole, which Williams and Rand (1977) suggest accounts for the presence of ornamentation in these species.

Most anoles, however, do not have conspicuous body ornamentation. Further, other anoles have small dewlaps but lack such ornamentation (e.g., *A. maynardi*). For these species, we have few definitive conclusions about the determinants of anole dewlap size (we reran analyses excluding conspicuously ornamented species and obtained qualitatively identical results, which we do not report). One possibility is that habitat illumination affects the evolution of dewlap size. Previous work has indicated that dewlap color varies as a function of habitat illumination (Fleishman, 1992); one might similarly expect the optimal size of the dewlap to be affected by the ability of other individuals to detect it. Six of the eight comparisons we made revealed that species in more poorly lit habitats had larger dewlaps, as one might predict. Although this result does not attain statistical significance, the results are suggestive, and the sample size is small. More detailed study, such as quantification of habitat illumination, may provide more data to test these hypotheses.

Many workers have postulated that dewlap color is important in species recognition, based primarily on differences in dewlap color among sympatric species (Williams and Rand, 1977; Echelle et al., 1971; Webster and Burns, 1973), as well as on experimental data (Losos, 1985; but see Jenssen, 1996). In Hispaniola, Rand and Williams (1970) discovered that each species could be uniquely identified by the coloration of its dewlap. A similar situation exists for other islands: in the communities that we examined on the three other islands in the Greater Antilles, only one pair of sympatric species (*A. grahami* and *A. opalinus*) has dewlaps of the same color or colors, and even in this case, the pattern of coloring is not identical.

Given that color alone may be sufficient for species recognition, one might inquire as to the significance of variation in dewlap size. Rand and Williams (1970) suggested that dewlap size served as a redundant cue for species recognition. Our analyses indicate no general patterns that would support this hypothesis, but it is possible that dewlap size is important for species

recognition in some communities but not others. Some data for both Cuba (Table 1) and Hispaniola (Table 2) are suggestive of such a relationship, but the best means of testing this hypothesis directly would be to conduct experimental studies. Video techniques, which work well with anoles (Macedonia and Stamps, 1994; Macedonia et al., 1994; see also Jenssen, 1970), now provide the capability of experimentally altering the size of the dewlap and directly assessing its role in species recognition.

By contrast, our analyses found no suggestion of a relationship between sexual size dimorphism and relative dewlap size of males. This result runs contrary to a study of Central American anoles (Fitch and Hillis, 1984). Given that Central American and Caribbean anoles differ in many ways, including life history, ecology, and morphology (Andrews, 1976, 1979; Irschick et al., 1997), this result may not be too surprising. Nonetheless, a detailed comparative study of mainland versus island anoles would prove interesting. Further, examination of Fitch and Hillis' data indicates that taxa in the same species' groups (following the designations of Savage and Guyer, 1989) are often similar in relative dewlap size, which suggests the possibility that Fitch and Hillis' statistical results are phylogenetically confounded. Consequently, when a phylogeny for Central American anoles becomes available, Fitch and Hillis' analyses should be reexamined.

Our analyses also reveal no relationship between relative dewlap size and signalling rate or habitat structure. The latter case exemplifies the importance of considering phylogenetic relationships in comparative analyses; our studies indicate that the seemingly significant result provided by nonphylogenetic analyses were an artifact of the inclusion of closely related species with similar phenotypes.

One factor we did not consider is the extent to which species differ in the movements they perform while displaying. Anoles have a rich repertoire of movements of the head, dewlap, body, and tail that they utilize during displays (Jenssen, 1977, 1978; Fleishman, 1992). Many of these movements are species specific, and some species have a larger repertoire than others. Consequently, the signalling value of the dewlap may be related to the display movements that a species performs. On one hand, such movements could compensate for a small dewlap; alternatively, movements and dewlap extension could interact to present a particularly effective signal. Further study of the relationship between display movements and dewlap size and configuration would prove very interesting.

Overall, this study fails to provide a general explanation for the vast diversity in dewlap size displayed by anoline lizards. We suspect that, because of the many contexts in which the dewlap is used and the alternative means of communicating the same message, more detailed studies will reveal that the determinants of dewlap size must be examined on a species-by-species basis.

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DEPARTMENT OF BIOLOGY, CAMPUS BOX 1137, WASHINGTON UNIVERSITY, SAINT LOUIS, MISSOURI 63130-4899. PRESENT ADDRESS: (LC) ANIMAL BEHAVIOR GRADUATE PROGRAM, UNIVERSITY OF CALIFORNIA, DAVIS, CALIFORNIA 95616. E-mail: (JBL) losos@biodec.wustl.edu. Send reprint requests to (JBL). Submitted: 25 July 1997. Accepted: 23 Oct. 1997. Section editor: A. H. Price.

APPENDIX. RELATIVE DEWLAP SIZE AND ECOMORPH DESIGNATION OF SPECIES INCLUDED IN THIS STUDY. Closely related species (following Jackman et al., 1997, in press, and references therein) are grouped together within an island. Some species do not belong to any ecomorph class. Letters indicate sets of closely related, ecologically similar species that differ in habitat illumination; numbers indicate light levels (ranked from dimmest to brightest).

	Relative dewlap size	Ecomorph ^a
Cuba		
ahli	0.958	TG
allogus a-0	1.065	TG
homolechis a-1	0.710	TG
mestrei	0.925	TG
ophiolepis	-1.145	GB
sagrei a-2	0.222	TG
allisoni	-0.423	TC
porcatus	-0.388	TC
alutaceus	0.396	GB
vanidicus	0.199	GB
angusticeps	-0.206	TW
guazumae	-0.239	TW
paternus	0.020	TW
bartschi ^b	-1.635	—
vermiculatus ^b	-1.407	—
equestris	-0.385	CG
luteogularis	-0.490	CG
loysiana	0.863	TR
lucius ^b	0.403	—
pumilus	-0.265	—
Hispaniola		
aliniger ^b	-0.402	TC
chlorocyanus	-0.242	TC
brevirostris	-0.256	TR
distichus	-0.279	TR
olssoni	0.579	GB
semilineatus	0.361	GB
bahorucoensis ^b	-1.217	GB
christophe ^b	0.481	—
etheridgei	-0.125	—
insolitus	0.914	TW
longitibialis	0.425	TG
Chamaelinorops barbouri	-1.219	—

APPENDIX. CONTINUED.

	Relative dewlap size	Ecomorph ^a
Jamaica		
grahami b-1	-0.024	TC
opalinus b-0	0.466	TC
lineatopus	0.704	TG
reconditus	0.685	—
garmani	0.086	CG
valencienni	0.460	TW
Puerto Rico		
cooki c-2	0.160	TG
cristatellus c-1	0.036	TG
gundlachi c-0	0.425	TG
krugi d-0	0.225	GB
poncensis ^b d-2	-0.948	GB
pulchellus d-1	0.050	GB
evermanni e-0	-0.127	TC
stratulus e-1	0.338	TC
cuvieri	0.233	CG
occultus	0.169	TW
Other Islands		
acutus	0.218	—
bimaculatus	-0.582	—
monensis	-0.614	—

^a CG = Crown-Giant; GB = Grass-Bush; TC = Trunk-Crown; TG = Trunk-ground; TR = Trunk; TW = Twig.

^b Species with conspicuous body coloration or patterning.