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The *Anolis* Dewlap: Interspecific Variability and Morphological Associations with Habitat

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The *Anolis* dewlap is a highly specialized display organ that shows considerable interspecific variability throughout the genus. Differences among many species in dewlap lepidosis provide several characters that are taxonomically useful. There are more or less distinct gorgetal and sternal scale-row arcs that differ interspecifically in number of rows, as well as in number, shape and size of the scales. There are small, closely set granular scales, here termed apicals, at the anterior and posterior corners of the dewlap. *Anolis* dewlaps are generally bordered by enlarged, imbricate marginals of a variable number of rows. Besides scalation, other interspecific differences occur in color, pattern and size of the dewlap.

Where seasonally dry climates limit reproduction to a short and concentrated annual breeding season, dewlaps are usually relatively large and brightly colored. In relatively aseasonal climates of tropical rainforests and cloud forests, dewlaps are often relatively small and, whereas some are brightly colored, others are a dull brown, tan or white. These differences in dewlap size are significantly correlated with another variable that is linked to seasonality of environments—sexual size difference (males are larger than females in seasonal environments). In some instances, there also may be compensatory development of bright colors in small dewlaps or large size in those that are dull colored.

MANY genera of iguanid lizards have conspicuous and distinctive organs, colorations or behaviors developed for visual display; the anole dewlap is one of the most specialized of these and is unique in various respects. Although characteristics of color and pattern of dewlaps have often been used in species descriptions of *Anolis* and are commonly used by many field-workers as means to identify species, most other morphological characteristics of dewlaps have received little study. Rand and Williams (1970) studied dewlap variability among eight sympatric species of *Anolis* at a single locality in Hispaniola, and considered the differentiation as it related to the premating isolation of the species. On the mainland of Middle America, however, considerably fewer species of *Anolis* are sympatric at most localities, and therefore the potential for interspecific competition and hybridization is greatly reduced. Our previous observations of *Anolis* in Middle and South America have suggested that interspecific variation in several morphological characters of dewlaps may be associated with seasonality of habitat. These observations prompted this study of the associations of lepidosis, color and size of dewlaps with environmental differences among approximately forty mainland species of *Anolis*.

Materials and Methods

For comparison of dewlap colors, patterns and lepidosis, anoles were placed against a standard background and individually photographed with 35 mm Kodachrome 25 film. In most instances the freshly anesthetized lizards were photographed just prior to preservation. The dewlap was spread to its fullest extent by erecting the hyoid cartilage at the anterior edge and holding it in place with a pin. In some instances live anoles were used and a collaborator held the animal immobile against the background and extended its dewlap by grasping the hyoid with pointed forceps while it was photographed.

Dewlap area was determined by extending the dewlap, holding the hyoid erect with forceps as already described, and then pressing the dewlap against a piece of paper on a flat background and tracing around its margin with a pencil. The area enclosed was measured with a polar planimeter to the nearest 10 mm².

Some dewlap measurements used herein are from earlier publications (Fitch, 1975; Echelle

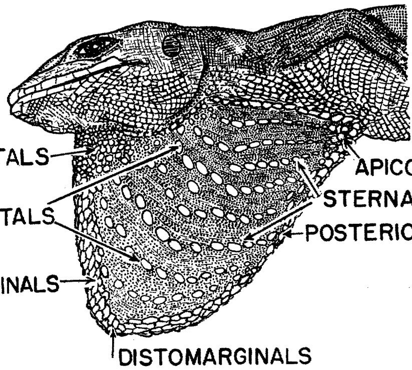

Fig. 1. Adult male *Anolis* with dewlap spread, showing types of dewlap scales with terminology proposed in text.

et al., 1978). In some instances slightly different figures have been used for the same species discussed in the above publications; in these cases, either additional dewlaps were measured or a larger series of the species was available from another locality. In the present study only adult males were included in the averages for dewlap measurements.

To test the utility of characters of dewlap lepidosis in the identification of species of *Anolis*, we performed a discriminant function analysis (BMDP7M of Dixon et al., 1981) with a matrix of four dewlap characters among six species for which we had relatively large samples. These species included one familiar North American species (*A. carolinensis*) and five little-known mesoamerican species (*A. lemurinus bourgeaei, A. cuprinus, A. isthmicus, A. quercorum* and *A. tropidonotus*).

Samples of 38 populations representing 37 taxa or unnamed species for which dewlap area was measured were analyzed for association of dewlap size and color with seasonality of habitat. The localities were divided into "seasonal" and "aseasonal" categories. These categories were defined by the vegetative communities at the collection localities. "Aseasonal" localities were those occupied by cloud forest or tropical rain forest; "seasonal" localities were those occupied by desert, thorn-scrub, deciduous forest or dry coniferous forest. This division was based upon the reproductive constraints of *Anolis*; reproduction by *Anolis* is potentially continuous in cloud forest and tropical rain forest, whereas reproduction is limited to the wet season in the other vegetative communities (Fitch, 1973a).

In order to evaluate the variation in dewlap size that is unexplained by variation in overall size, we performed a principal components analysis (BMDP4M; Dixon et al., 1981) on the variables snout–vent length and dewlap area. The first principal component accounts for the largest axis of variation, in this case the general correlation of body and dewlap size (Echelle et al., 1978). The second axis then provides a contrast of the variables.

Results

Differentiation of dewlap scales.—There is differentiation of scales on particular areas of the dewlap, but scale types tend to grade from one to another. In a description of dewlap scalation it is necessary to specify the part of the dewlap that is being considered. Because there are no established names for these various areas of *Anolis* dewlaps, we propose the following terminology (as shown in Fig. 1) for convenience in description.

1) Marginals: on the margin of the dewlap, consisting of:
   a) anterior marginals;
   b) distomarginals;
   c) posterior marginals.
2) Gorgetals: below the throat on the base of the dewlap, and in successive rows outward, separated by areas of bare skin that are usually brightly colored.
3) Sternals: below the thoracic area on the base of the dewlap, and in successive rows outward, separated by areas of bare skin.
4) Apicogorgetals: small, irregular, crowded scales, between which no skin is exposed, at the anterior corner of the dewlap.

TABLE 1. JACKKNIFED CLASSIFICATION MATRIX FOR SIX SPECIES OF *Anolis* FROM A DISCRIMINANT FUNCTION ANALYSIS BASED ON FOUR COUNTS OF DEWLAP LEPIDOSIS.

Species	Percent correctly classified	Number of specimens classified as: A	B	C	D	E	F
A. carolinensis (A)	100.0	16	0	0	0	0	0
A. quercorum (B)	88.2	0	15	2	0	0	0
A. tropidonotus (C)	100.0	0	0	19	0	0	0
A. bourgeaei (D)	94.4	0	0	0	17	1	0
A. isthmicus (E)	100.0	0	0	0	0	19	0
A. cuprinus (F)	100.0	0	0	0	0	0	17

5) Apicosternals: similar to apicogorgetals, but at the posterior corner of the dewlap.

A combination of four characters of dewlap lepidosis was highly effective in discriminating among the six species tested (Table 1). Using only the number of horizontal gorgetal-sternal rows, mean number of scales per horizontal row, number of marginal series and modal number of anterior marginal pairs, 97.2% of 106 individuals of the six species were correctly identified by the jackknifed classification functions. All four characters had highly significant F's-to-enter (all above $F = 10$; $df = 5, 100$; $P \ll .001$). Means and standard errors for these characters are presented for 18 species in Table 2.

Although these characters are clearly of systematic value, there are irregularities that at times prevent consistent counts. The scales of both gorgetal and sternal rows are curved in convex arcs (Fig. 1) rather than aligned in straight rows. The two sets of curved rows are often offset rather than aligned, causing doubt as to which gorgetal row is the counterpart of any sternal row or vice versa. Within both gorgetal and sternal series there are further irregularities such as single isolated scales or series of several scales forming short extra rows. The numerous minute apicogorgetal and apicosternal scales tend to be arranged in rows, but with many irregularities. It is necessary to eliminate these minute scales of the apical regions from the counts, but deciding where to begin or end a count is difficult. The minute granular apical scales at the corners grade into the larger scales of the central dewlap by almost imperceptible stages. The criterion for recognizing gorgetals and sternals is the occurrence of exposed skin between the scales. Apicogorgetals and apicosternals lack such noticeable interspaces even when the dewlap is extended. Admittedly this criterion is somewhat subjective. In a young male with a dewlap smaller than average for the species, basal scale rows may be closely set with no interspaces, whereas the same male as an adult, with a larger dewlap having more elastic skin, would show bare areas exposed between these scale rows.

In a typical dewlap the largest scales are near the center and are in the sternal rows, whereas at the base, and especially at the anterior and posterior corners, scales are small, granular, and crowded. The cartilage extending posteriorly from the hyoid is a long, flexible rod along the anterior edge of the dewlap, and it is ensheathed in unelastic skin, with large, flattened, imbricate scales, the anterior marginals and distomarginals. These are most often in sets of three pairs, but vary between one and four or more pairs. Along the posterior margin of the dewlap the number of scale-pairs is generally reduced, and there are areas of exposed skin between the scales. This part of the dewlap is elastic and contracts when the organ is folded. In some species scales may become minute or largely suppressed in the central part of the dewlap. The relative amount of scale surface and exposed skin in a dewlap varies greatly depending on the species. The scalation also is highly variable, and may be fine or coarse, depending partly on the type of ventral scalation in the species. Both the number of scale rows and the number of scales per row differ greatly between species but exhibit relatively minor variation within species.

Scale counts of dewlaps, such as those shown in Table 2, reflect the type of ventral scalation found in the species (whether fine or coarse), and also reflect the relative size of the dewlap. Fine-scaled species with large dewlaps (i.e., *A. cuprinus, A. villai*) have several times as many dewlap scales as those that are coarse-scaled and have small dewlaps (i.e., *A. humilis, A. sericeus*). The counts of dewlap scales listed in Table 2

TABLE 2. SCALE COUNTS OF DEWLAPS OF 18 SPECIES OF *Anolis*. Counts presented are means; standard errors are in parentheses.

Species	N	Horizontal gorgetal-sternal scale-rows	Mean number scales per horizontal row	Number of marginal series	Apico-gorgetals[1]	Apico-sternals[1]	Modal number anterior marginal pairs	Locality
A. bourgeaei	18	8.24 (0.19)	11.0 (0.48)	35.05 (1.02)	—	—	3	Santa Barbara, Honduras
A. carolinensis	16	11.94 (0.57)	19.1 (0.94)	43.48 (0.80)	20, 34	10, 21	3–4	Texas, USA
A. cristatellus	1	14	19.9	47	17, 21	—	3	Limon, Costa Rica
A. cupreus	11	9.00 (0.38)	20.5 (1.01)	56.73 (1.92)	—	—	3	Santa Rosa, Guatemala
A. cuprinus	18	11.53 (0.46)	18.7 (0.65)	62.39 (0.95)	—	—	2	Oaxaca, Mexico
A. dunni	1	11	15.4	42	15, 15	12, 5	1	Guerrero, Mexico
A. gadovi	1	10	19.6	50	13, 18	10, 6	1	Guerrero, Mexico
A. gemmosus	1	7	24.3	95	16, 14	—	3	Pichincha, Ecuador
A. humilis	9	9	12.8	41	—	—	—	Limon, Costa Rica
A. isthmicus	19	9.00 (0.36)	18.0 (0.69)	54.42 (0.98)	—	—	3	Oaxaca, Mexico
A. liogaster	1	5	14.0	40	—	—	1	Guerrero, Mexico
A. nebuloides	2	8–9	16.5	49	9, 9	7, 3	3	Oaxaca, Mexico
A. quercorum	17	6.82 (0.20)	13.3 (0.50)	44.24 (0.82)	—	—	2	Oaxaca, Mexico
A. sericeus	1	9	12.1	33	9, 9	4, 3	—	Oaxaca, Mexico
A. subocularis	1	10	14.1	57	5, 5	—	2	Guerrero, Mexico
A. taylori	1	15	13.1	43	16, 22	20, 17	2	Guerrero, Mexico
A. tropidonotus	19	7.79 (0.18)	8.0 (0.19)	39.84 (0.77)	—	—	2	Santa Barbara, Honduras
A. villai	1	17	21.8	52	6, 9	—	3	Great Corn Island, Nicaragua

[1] The first number represents a count along the rim of the dewlap; the second number represents the count from the rim across the base to a point where exposed skin shows between the scales.

constitute more or less diagnostic characters between species. We suggest that such dewlap-scale counts should be included routinely in technical descriptions such as those of new species.

Color, pattern and size of dewlaps.—Color and pattern of dewlaps show varying degrees of specialization among *Anolis*. An anole having a dewlap in which both the scales and the exposed skin areas between them match the usual pale gray or whitish of the rest of the ventral surface probably has the least effective display organ, but also is less vulnerable to predation than one having a more colorful dewlap. Even a relatively inconspicuous dewlap may serve effectively in display, as the stereotyped bobbing movements call attention to the spread gular fan. However, in a more typical dewlap the loose skin between the scales is brightly colored, often red, pink or orange. When it is spread, the broken light lines of the scale rows, contrasting with colored skin between, render the display more conspicuous, but when the organ folds, the colored skin is concealed.

As a further specialization, each scale or each horizontal row of scales may be enclosed in an area of different color or shade from the remainder of the dewlap skin. The marginal area of the dewlap may be of a different color (often paler) than the remainder. Some bright colored dewlaps are rendered even more conspicuous by having a central mark or spot of contrasting color. For example, *A. sericeus* has an orange dewlap with a round central indigo spot. The dewlap is bright and has a contrasting color pattern, but it is relatively small. Many other species also have bicolored or tricolored dewlaps. For example, in *A. cupreus* a small basal area is deep amber and a larger outer area is rose.

The size of the dewlap has obvious bearing on its effectiveness in display; the relative and actual size varies markedly among the species. The dewlap arises from the chin below the anterior corner of the eye or below mid-eye, but in display the anterior rounded edge may project beyond the snout as the hyoid is extended forward. The posterior end of a small dewlap is opposite the axilla, but a large dewlap may extend to mid-abdomen. A typical dewlap is about twice the depth of the anole's head, but shape varies; some are relatively shallow and others are deep. Both size and shape of the dewlap are undoubtedly related to the type of display, but as yet displays are known in only a few species. To hold its extended dewlap clear of the substrate, the anole must stand high and tip its head back. In displaying, *A. nebulosus* at times stands erect on its hind legs, gaining ample space for the dewlap in the course of its bobbing movements (Jenssen, 1970).

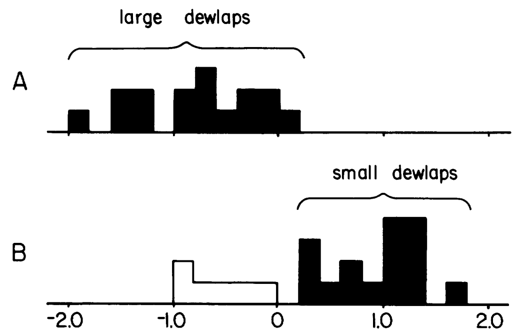

Fig. 2. Scores along principal component II for 38 species or populations of *Anolis* (Table 4). A positive score on PC II indicates a small dewlap relative to body size, whereas a negative score indicates a large dewlap. A) *Anolis* from highly seasonal environments. B) *Anolis* from relatively aseasonal environments. The open portion of the histogram represents the six species from aseasonal environments with relatively large dewlaps.

Among the species studied, *Anolis* that occur in seasonal environments have relatively larger dewlaps than those that occur in aseasonal environments. This is illustrated in Fig. 2, where snout–vent length is contrasted against dewlap area along principal component II. The difference in mean scores on PC II for seasonal versus aseasonal species is significant at $P < .001$ ($t = 5.96$, $df = 37$). Because the loadings for PC II (Table 3) are positive for snout–vent length (0.232) and negative for dewlap area (−0.232), a species with a high positive score on PC II has a relatively small dewlap with respect to its body size, whereas a species with a high negative score on this axis has a large dewlap with respect to its body size. Species with high negative scores on PC II include *A. cuprinus, A. cupreus, A. isthmicus, A. nebuloides, A. nebulosus, A. subocularis* and *A. quercorum.* All of these species live in seasonally dry climates, where reproduction is limited to the wetter part of the year, with the breeding season relatively short and concentrated. Each of these same species also has a highly colorful dewlap. Species with relatively small dewlaps include *A. bourgeaei, A. gemmosus, A. heteropholidotus, A. lemurinus* (Costa Rica), *A.*

TABLE 3. MORPHOMETRIC AND MULTIVARIATE MEASURES OF *Anolis* FROM SEASONAL AND ASEASONAL ENVIRONMENTS, AND FACTOR LOADINGS ON PRINCIPAL COMPONENTS I AND II.

Character	Seasonal $\bar{x} \pm s_{\bar{x}}$ (range) N = 16	Aseasonal $\bar{x} \pm s_{\bar{x}}$ (range) N = 22	Factor loadings PC I	Factor loadings PC II
Snout–vent length (mm)	56.7 ± 3.75 (39–85)	54.0 ± 2.57 (34–82)	0.973	0.232
Dewlap area (mm²)	411.4 ± 53.3 (129–786)	250.8 ± 34.3 (54–604)	0.973	−0.232
Score on PC II	−0.801 ± 0.147 (−1.918–0.074)	0.506 ± 0.175 (−0.987–1.633)	—	—

TABLE 4. TYPE OF ENVIRONMENT AND CHARACTERISTICS OF DEWLAPS AND BODY SIZE AMONG VARIOUS SPECIES OF *Anolis* FROM MIDDLE AND SOUTH AMERICA. N_1 is the sample used to calculate dewlap area; N_2 is the sample size for sexual size difference. S = seasonal, A = aseasonal; Bl = blue, Br = brown, O = orange, P = purple, R = red, W = white and Y = yellow.

Species (N_1, N_2)	Seasonality of environment		SV length (mm)	Dewlap area (mm²)	PC I	PC II	Dewlap color		Sexual size difference (male SVL/female SVL) × 100		
	S	A					Bright	Dull	>110	100–110	<100
A. aequatorialis (2, 10)		X	82	604	1.769	1.183		Br		102	
A. aquaticus (9, 19)		X	67	580	1.125	−0.987	O		113		
A. attenuatus (2, 42)	X		85	786	2.362	−0.325		Br		105	
A. bourgeaei (8, 37)		X	66	370	0.537	1.153	R				97
A. carpenteri (2, 20)		X	39	150	−1.084	−0.815	O				95
A. chloris (2)		X	59	400	0.345	−0.311		W	—	—	—
A. cuprinus (7, 37)	X		67	665	1.348	−1.918	R		136		
A. cupreus macrophallus (17, 86)	X		46	268	−0.504	−0.973	O/R		121		
A. cupreus spilomelas (38, 80)	X		43	250	−0.668	−1.263	O/R		119		
A. dollfusianus (26, 96)	X		39	129	−1.139	−0.585	Y/O			106	

TABLE 4. (CONTINUED.)

Species (N_1, N_2)	Seasonality of environment		SV length (mm)	Dewlap area (mm^2)	PC I	PC II	Dewlap color		Sexual size difference (male SVL/female SVL) × 100		
	S	A					Bright	Dull	>110	100–110	<100
A. dunni (1, 9)	X		58	350	0.175	0.074	R		120		
A. gadovii (8, 22)	X		71	560	1.228	−0.119	P		113		
A. gemmosus (24, 66)		X	63	318	0.285	1.236	Y/Bl			106	
A. heteropholidotus (2, 17)		X	50	190	−0.554	0.530	R				92
A. humilis (29, 261)		X	37	100	−1.293	−0.592	R/Y				95
A. intermedius (9, 339)		X	46	110	−0.918	0.758		W		101	
A. isthmicus (6, 24)	X		52	390	0.047	−1.337	O/Y		126		
A. lemurinus CR* (3, 29)		X	55	204	−0.323	1.188	R				97
A. "*lemurinus*" EC* (1)		X	70	412	0.802	1.341	O		—	—	—
A. "*lemurinus*" ES* (2, 16)	X		73	600	1.410	−0.233	R			107	
A. limifrons (65, 568)		X	37	72	−1.366	−0.285		W/Y			97
A. lionotus (3, 43)		X	72	415	0.887	1.633	Y		118		
A. megapholidotus (3, 42)		X	48	177	−0.665	0.348	R			102	
A. nebuloides (2)	X		47	335	−0.290	−1.545	P		—	—	—
A. nebulosus (4, 102)	X		43	190	−0.825	−0.605	Y			100	
A. nigrolineatus (14, 29)		X	51	137	−0.654	1.273		W		106	
A. pentaprion (1, 10)	X		74	650	1.580	−0.618	R		123		
A. peraccae (16, 3)		X	50	118	−0.742	1.319		W		107	
A. polylepis (7, 88)		X	51	255	−0.345	−0.020	O			108	
A. quercorum (16, 18)	X		41	196	−0.887	−0.995	P		113		
A. sericeus N (10, 20)		X	39	54	−1.336	0.237	O/Bl			100	
A. sericeus S (24, 81)	X		43	150	−0.930	−0.167	O/Bl		111		
A. sminthus (7, 15)		X	45	80	−1.035	0.925	R				88
A. subocularis (14, 68)	X		52	405	0.086	−1.502	O		132		
A. taylori (13, 66)	X		74	658	1.601	−0.706	P		126		
A. tropidolepis (21, 473)		X	51	160	−0.593	1.021	R			101	
A. tropidonotus (10, 30)		X	55	245	−0.216	0.738	R		123		
A. villai (9, 59)		X	54	366	0.062	−0.750		Br	112		

* *A. lemurinus* CR = *A. lemurinus* from Costa Rica; *A.* "*lemurinus*" ES = supposed *A. lemurinus* from El Salvador; *A.* "*lemurinus*" EC = undescribed species similar to *A. lemurinus* from Eucador.

"*lemurinus*" (Ecuador), *A. limifrons, A. nigrolineatus, A. peraccae, A. sminthus, A. tropidolepis* and *A. tropidonotus*. In contrast with those of the first group, these are species that may breed through most of the year or all of it in cloud forest or rainforest habitat. Several have colorful dewlaps, but in others, including *A. nigrolineatus* and *A. peraccae*, dewlaps are dull and whitish. Table 4 lists the scores on PC I (overall size) and PC II (contrast of snout–vent length and dewlap size), as well as dewlap colors and seasonality of environment, for 38 species and populations of *Anolis*.

The association of relative dewlap size with seasonality of the environment is apparent not only between species, but within species as well. For instance, in Table 4 two samples of *A. sericeus* are listed; one of these (designated northern) is from the relatively aseasonal area at the bend of the Gulf of Mexico in southern Veracruz, Mexico. The other (designated southern) is from a highly seasonal area on the Pacific coast of Chiapas, Mexico. Note that the sample from the Chiapan population had an average dewlap area almost three times that of the population from Veracruz, despite the fact that the mean snout–vent length of the Chiapan sample was only slightly larger than that of the sample from Veracruz.

Discussion and Conclusions

The anole dewlap serves in aggressive displays that may function in courtship, territorial defense, or species recognition (Carpenter, 1967). The dewlap was present in the ancestral *Anolis*, as evidenced by its presence in *Chamaeleolis, Chamaelinorops* and *Polychrus*, and it remains a conspicuous organ in almost all of the extant species of *Anolis*.

In juvenile male anoles there is ordinarily no indication of the future dewlap, and its development is concurrent with other changes accompanying growth and maturation. The skin of the dewlap region becomes loose, elastic and colored, and scales are altered in shape. In some species even hatchling males show a trace of the dewlap color, and development of the dewlap is gradual, whereas in others development is fairly abrupt with the onset of adolescence (Echelle et al., 1978).

Some species of *Anolis* develop bright colors on dewlap scales. Ordinarily the scales are of the same whitish color as the remainder of the ventral surface, so that when the dewlap is collapsed there is little or no bright color to be seen, even from ventral view. The color may extend only onto the edges of the scales, or may include entire scales.

Female anoles show all gradations, from those species in which there is no trace of a dewlap to those having a trace of male color, and those having very small dewlaps up to those having dewlaps almost as large as those of their male counterparts. Presumably, in each instance, the relative development of male and female dewlaps is closely associated with the species' social structure and behavior, but such associations have not been well demonstrated.

In a study of species recognition and dewlap function, primarily in insular anole faunas, Williams and Rand (1977) found significant correlation between complexity of fauna and trend of dewlap variation. On islands with relatively simple anole faunas, dewlaps tended to be similar in color (often orange) and pattern (lacking contrasts), and served functions other than species recognition (such as territoriality or courtship). Where numerous species occurred on the same island, dewlap color tended to be diverse and diagnostic. Perhaps mainland faunas have similar trends; rainforest species often occur together with several in sympatry and they tend to develop more diverse dewlaps than are found in those species that occur alone in marginal xeric or cold (montane) areas.

In a study of sexual size differences in the mainland anoles, Fitch (1976) found that species inhabiting the most stable tropical environments, rainforest and cloud forest, consistently had the sexes near the same size, with females somewhat larger in most. In contrast are those species subjected to sharply seasonal climates, with a long dry season during which reproduction is suspended or reduced to a low level. In such species the average size of males is consistently much larger than the average size of females. A plausible explanation is that in the more stable environments, the population structure is stable and throughout the year maintains a fairly constant ratio of all size- and age-groups (Fitch, 1973b). Territories are relatively permanent, and there is a gradual replacement of individuals. In contrast, the short reproductive period in seasonal climates produces intraspecific stress, as a newly matured cohort of adults, constituting the bulk of the breeding population, competes for territories and mates. Success in male combat and display are at a premium. The sexual size differences of the species in this study are listed in Table 4. The mean sexual size difference of the anoles from seasonal localities (SV length of males 117.2% that of females) is significantly larger than the mean sexual size difference of the anoles from aseasonal localities (104.1%; $P < .001$, $t = 3.78$, $df = 34$).

It might be expected that in species of seasonal climates, relatively large male size would be accompanied by a suite of other characters associated with effective display. These characters might include a vigorous display, a relatively large, brightly colored dewlap with contrasting colors, and complex dewlap lepidosis. Table 4 lists 38 species or populations with their pertinent characters, insofar as known to us. Type of display is not included because it has been recorded for only a few of the kinds listed. The correlation of relative sexual size difference with scores on PC II ($r = -0.42$, $df = 34$) is significant at $P < .01$.

There is a strong tendency for species in seasonal climates to have relatively large dewlaps, and those with dewlaps smaller than average nearly all occur in relatively aseasonal climates (Fig. 2). The species that occur in seasonal climates all have brightly colored dewlaps that are predominantly red, orange, pink, purple or yellow. Some of the species in aseasonal climates have these same bright colors but others have dull dewlaps, often brown, tan or dull white. Dewlap pattern, contrasting or relatively uniform, and lepidosis, complex or simple, do not show association with climate with the information available.

While size and color of dewlaps are strongly associated with seasonality of habitats, there may be some compensation for weak development of one of these variables by strong development of the other. For instance, three of the species from aseasonal environments that have medium to large dewlaps (*A. aequatorialis, A. princeps, A. villai*) also have brown or white dewlaps. It also should be noted that while there probably is strong selection pressure in seasonal environments for large, colorful dewlaps, the reverse is not necessarily true in aseasonal environments. Because dewlaps play an important behavioral role in premating isolation of anoles, one would not expect all sympatric *Anolis* in an aseasonal environment to have small, dull-colored dewlaps. Selection pressures resulting from interspecific interactions probably favor a diversity of dewlap colors and sizes where several species occur in sympatry. This may explain the six species from aseasonal areas with relatively large dewlaps shown in Fig. 2. As a result of this diversity, in many relatively aseasonal areas (Duellman, 1978), many species of *Anolis* can occur sympatrically, each with a morphologically distinct dewlap.

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