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A Comparative Display Analysis of the *Anolis brevirostris* Complex in Haiti

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ABSTRACT.—The stereotyped head bob displays of three *Anolis* sibling species, formerly recognized only as *A. brevirostris,* were quantitatively analyzed from 736 filmed displays by 46 subjects. The three species are sequentially distributed along the west coast of Haiti, with *A. websteri* in the north, *A. caudalis* in the middle, and *A. brevirostris* in the south. It has been hypothesized that a behavioral isolating mechanism, such as the head bob displays, was serving to separate the species. Our data support this possibility.

Each species' behavioral repertoire contained two categories of homologous and species-unique displays: the Type A and B displays. A single Type A display pattern was found in each repertoire, and it served as the species' signature display. The Type B displays were more complex than the A displays, and in *A. brevirostris* and *A. websteri* were represented by two and three different variations, respectively. Each species' A display resembled that of its siblings; however, discriminant analysis procedure clearly discriminated between the three A display patterns. Likewise, the B display patterns of the combined sibling repertoires were also clearly separated by the discriminant analysis procedure, confirming their species uniqueness. Interspecific comparisons showed the largest differences in homologous displays to occur among geographically adjacent species, especially between the displays of *A. websteri* and *A. caudalis.* Character displacement may have enhanced these differences.

The study of allopatric and parapatric sibling species provides a unique opportunity to gather information on the mode of evolution. These species represent recent products of micro-evolutionary events. As such, any ecological or behavioral features which reflect obvious interspecific differences are likely to have been directly involved in the process of reproductive isolation; shifts in traits not participating in the speciation process would presumably be either parallel among the sibling species or diverging at a slower rate than those functioning as isolating mechanisms.

The present investigation deals with the Hispaniolan lizard, *Anolis brevirostris,* recently found to be at least three sibling species (Webster and Burns, 1973). The three species are contiguously distributed along Haiti's western coast, with no major geographic or ecological barriers separating their populations. Without electrophoretic evidence and knowledge of collection site, no one morphological trait is unequivocally diagnostic for species identification. The most distinctive morphological difference among the three species is the color of the extensible throat fan, or dewlap. Because the dewlap is a signalling structure used for social communication, Webster and Burns (1973) suggested that a behavioral isolating mechanism was preventing genetic exchange between adjacent sibling species.

For anoline lizards, dewlap movement and its flash of skin color is combined with vertical head bobs to produce stereotyped and species-unique visual displays (Jenssen, 1977). These displays are used in various social contexts, including courtship. It is in this last context that the courting male's species-unique head bob cadence and pulses of dewlap color may be assessed by a female. Female choice then becomes a mechanism for reproductive isolation; if the male's display does not meet her criteria, she will avoid copulating with that male.

Our study is a first step in evaluating the hypothesis that behavioral isolating mechanisms operate within the species complex. The objectives are a quantitative analysis of each species' display repertoire and a comparison of these repertoires for the identification of consistent, species-unique features which might serve in species recognition and mate selection.

METHODS AND MATERIALS

Subjects.—The three sibling species are relatively small, stocky anoles (males $\leq$51 mm SVL, females $\leq$47 mm SVL) that have faint dark markings on a gray-brown ground color. The most unique body marking of this group is an "ocellus," a dark circular patch on each side of the nuchal area (Arnold, 1980). Typically, these bark-colored anoles inhabit a semi-arboreal habitat, commonly being found on the trunks and larger limbs of trees in mesic to xeric woods. They appear to prefer the taller trees which surround villages, but will also occupy the low and often dense *Acacia* shrub (Arnold, 1980).

The three anoline species recognized in the Webster and Burns (1973) study were described by Arnold (1980). They are: *Anolis websteri,* the northernmost species; *Anolis caudalis,* the centrally distributed species; and *Anolis brevirostris,* the southernmost species (Fig. 1). In the following, "brevirostris" designates the three sibling species while *A. brevirostris* refers to only the southernmost species.

Male dewlap color appears to be the most diagnostic external character among the siblings. Colors contrast most between species in areas of interspecific contact. *Anolis websteri* dewlaps are uniformly orange or orange with a narrow yellow margin. Dewlap color of *A. caudalis* is pale white or sometimes yellow at the websteri-caudalis interface, but is

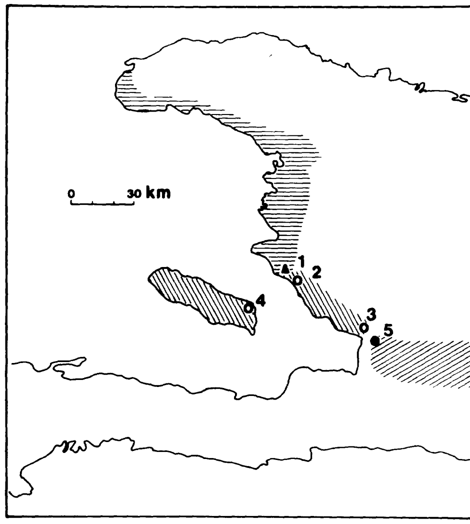

FIG. 1. Known species distributions and collecting sites for *A. websteri* (1, Montrouis), *A. caudalis* (2, Trou Forban; 3, Source Matelas; 4, Ile de la Gonave), and *A. brevirostris* (5, Daspinasse).

variable over the remainder of its range. Webster and Burns (1973) reported a clinal gradation from pale white or yellow in the North to orange in the South for *A. caudalis.* However, the senior author found *A. caudalis* dewlaps ranging from white to mostly orange with a slight white margin within one kilometer of *A. websteri.* Dewlap color in *A. caudalis* at the caudalis-brevirostris interface is bright orange. In contrast, *A. brevirostris* dewlaps are monochromatic in pale shades of peach, yellow, and gray.

Collections.—The display analysis of the sibling species was based on three collections. The first was collected and sent alive to the Virginia Polytechnic Institute and State University laboratory in 1972 by T. P. Webster; these lizards included all three species and were taken from the two contact zones along Route 100 of Montrouis-Trou Forban in the north and Source Matelas-Daspinasse in the south (Fig. 1). The second and third collections were made in the same Montrouis-Trou Forban zone in 1975 and 1977; the 1977 collection also included specimens from Ile de la Gonave.

Methods.—In the laboratory, lizards were toe clipped for permanent identification and were housed in glass-fronted wooden enclosures which measured 1.2 × 0.6 × 0.7 m. Each enclosure held 1–4 males and 3–4 females and contained artificial vegetation, large tree stumps, and branches. Two fluorescent lights set on a 12 L : 12 D cycle hung above each cage. Each day the lizards were fed *Tenebrio* larvae and small crickets which had been dusted with calcium lactate and vitamins. Occasionally, field sweepings of local insects supplemented this diet. Water was sprayed onto the foliage daily as well as being available in shallow dishes.

Displays were recorded, both in the field and lab, using a Nizo S80 super 8 camera set at 18 frames/s. To film the display behavior of a male, the subject was placed in a filming enclosure with the same dimensions and similar habitat as its holding cage. Floodlights provided light for filming and added heat for lizard thermoregulation. Initially, the subject shared the enclosure with several females; this situation produced both non-directed and male-female behaviors. After a sufficient sample of displays had been filmed within these contexts, another male was introduced to elicit displays within a male-male context.

During a combined period of three months in 1975 and 1977, extensive field notes and films were made on social behavior of *A. websteri* and *A. caudalis* in and around the contact zone. An attempt was made to record the displays of known individuals. This was done by either capturing and paint marking particular individuals, or by filming a continuous sample of displays from a particular uncaptured individual before shifting to the next subject. Shifts between lizards were noted in a film notebook or directly on the film cartridges after exposure. There were also isolated instances of filming particular kinds of behavior as they were fortuitously encountered; in these cases the displayers' identities were unknown.

The displays of free-ranging individuals were filmed during naturally occurring behavior as males moved within their territories. The responses of residents to released, paint-marked intruders (both males and females) in their territories were also filmed. As in the lab, an attempt was made to record display behavior from a wide spectrum of social contexts. In this way an attempt was made to sample the complete repertoire of each species' head bob displays.

Film Analysis.—Each display was analyzed frame-by-frame using a graphic representation for head amplitude and dewlap extension through time (see also Jenssen and Hover, 1976). To create the graph, the first cinema frame of a display is projected onto the first vertical line of a piece of graph paper. Along this line the position of the lizard's snout is marked, as well as the extent of dewlap extension from the margin of the throat. The film is then advanced to the second frame and the new head and dewlap reference points marked on the next vertical line of the paper. This procedure is repeated until all frames depicting the display have been sequentially referenced on the graph paper. The points on the graph paper depicting frame-to-frame head amplitude are then connected to produce the display-action-pattern (DAP) graph, and the dewlap points are connected to show downward deflection of the dewlap in relationship to the concomitant head amplitude. In this way the y-axis gives relative head and dewlap amplitude, and by connecting the consecutive reference points, the x-axis gives the dimension of movement (passage of time). Thus a quick up-and-down head bob will look like a "spike" when graphed, and a bob which is held before the head is lowered will have a "plateaued" appearance. If the dewlap is extended during the display, it appears on the DAP graph under the corresponding head bob representation. Dewlap extension is a downward vector along the y-axis, and dewlap retraction is an upward vector along the same axis.

All displays were made up of head bobs separated by interbob pauses. These two natural events within the displays were designated as "units" to facilitate a quantitative analysis. Durations of the head bob units were derived by counting the cinema frames which recorded the initial rise of the head through to its lowering. The interbob pause durations came from the number of frames comprising the period between bobs. Within a display, units were consecutively numbered. Because the bobs were interspersed with pauses, odd-numbered units represented bob durations and even-numbered units represented interbob pause durations.

The following variables were recorded for each display: (1) identity of displayer; (2) collection site; (3) display type; (4) field or lab filmed; (5) unit durations; and (6) social context. Quantitative analysis of the display variables was then carried out with the Statistical Analysis System (Barr et al., 1979) and Biomedical Computer Programs (Dixon, 1975).

Results

Display Repertoire

From the analysis of 736 filmed displays by 46 males (Table 1), we found that the repertoires of *A. websteri*, *A. caudalis* and *A. brevirostris* each contained two basic kinds of bob patterns, designated the Type A and Type B displays (Figs. 2 and 3). The Type A displays were always performed with five bobs, but could have one or two optional bobs added to the end. The dewlap, if extended at all, appeared after the head bobbing. In contrast, the Type B displays contained more head bobbing than the Type A displays, with frequent

TABLE 1. Summary of number of filmed displays used in the analysis.

Collecting Locality	Where Filmed	Number of Subjects	Display Type A	Display Type B
A. websteri				
Montrouis	Lab	9	190	85
Montrouis	Field	9	44	9
A. caudalis				
Trou Forban	Lab	9	41	50
Trou Fobran	Field	7	23	21
Ile de La Gonave	Lab	6	47	64
Source Matelas	Lab	2	29	19
A. brevirostris				
Daspinasse	Lab	4	71	43

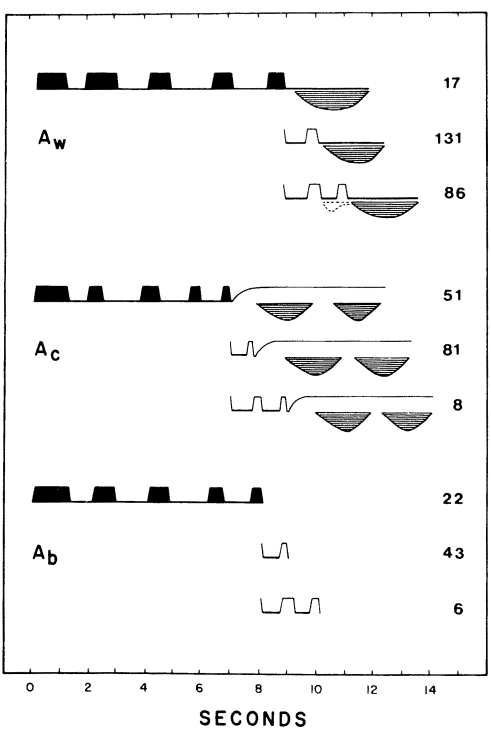

FIG. 2. Mean durations for Type A displays of *A. websteri* (Aw), *A. caudalis* (Ac), and *A. brevirostris* (Ab), showing the five bob core display (blocked in head bobs) and optional bobs (outlined bobs). Dewlap extension is depicted beneath line of head bobs. Sample sizes are given to the right.

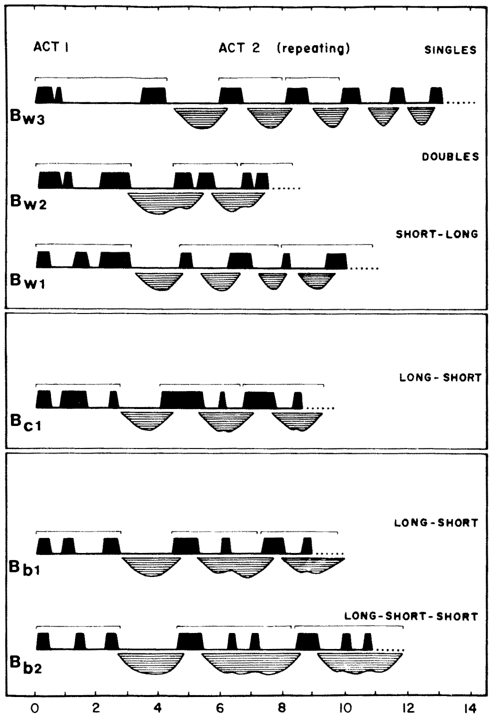

FIG. 3. Mean durations for Type B displays of *A. websteri* (B_{w1-3}), *A. caudalis* (B_{c1}), and *A. brevirostris* (B_{b1-2}). Phrase to right describes Act 2 repeating bob pattern.

TABLE 2. Kinds and number of male displays observed in each of three contexts for *A. websteri*, *A. caudalis*, and *A. brevirostris*. Table includes film and field observations.

Species	Context; Type A Displays		
	non-directed	male-male	male-female
A. websteri	81	39	103
A. caudalis	39	29	101
A. brevirostris	3	22	3
	Context; Type B displays		
	non-directed	male-male	male-female
A. websteri	0	19	31
A. caudalis	0	43	87
A. brevirostris	0	14	3

dewlap pulsing during the head bob sequence. In addition the B displays featured a repeating element of head bobs and dewlapping which began after the first three bobs (Fig. 3). Depending on species, there were one to three versions of the Type B display: *A. caudalis* had one (labeled B_{c1}), *A. brevirostris* had two (labeled B_{b1}, B_{b2}), and *A. websteri* had three (labeled B_{w1}, B_{w2}, B_{w3}).

Type A Displays

All three sibling species performed their Type A displays in the non-directed, male-male, and male-female contexts (Table 1). It was the only display type used for non-directed displaying, a situation in which there was no apparent overt social interaction; the nearest potential recipient of the display was not to be seen, at great distance to the displayer, or not the apparent object of the display (i.e. behind the displayer). Displaying within the non-directed context most frequently occurred when a patrolling male periodically stopped as he moved about his territory, but also occurred after eating, after defecating, and when moving away from a female after copulation. The Type A displays were also used during male-male aggressive encounters, when males were approaching females during courtship, and while males were in copula.

Descriptively, the A displays of the three sibling species were similar in pattern (Fig. 2). Because virtually every A display contained five bobs, we viewed this portion of the A display as its "core." Frequently, however, the lizards added one or two bobs onto the end of the display's core. This happened in 94, 64, and 69% of the *A. websteri*, *A. caudalis*, and *A. brevirostris* A displays, repsectively (Fig. 2, listed sample sizes). The number of dewlap pulses which followed the head bobbing of the A displays was also variable (0–5), and showed some diverging interspecific trends (Fig. 4). Details of intra- and interspecific analyses follow.

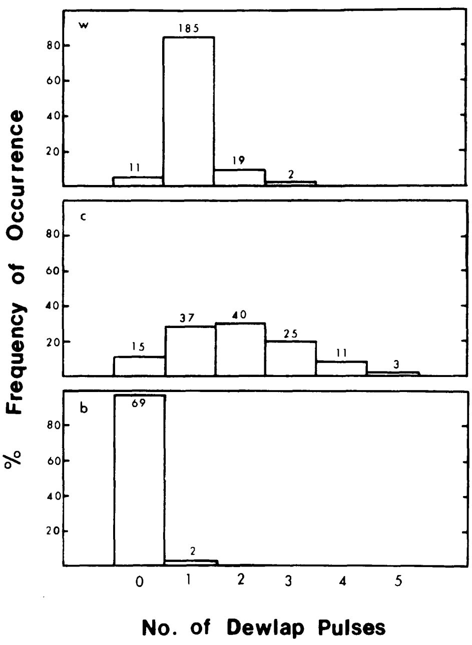

FIG. 4. The number of dewlap pulses performed at the end of the Type A displays of *A. websteri* (w), *A. caudalis* (c), and *A. brevirostris* (b). Numbers over bars are sample sizes.

Websteri.—The number of head bobs performed varied from five to seven, with displays of six head bobs being most common. The core display of *A. websteri* was the longest of the three species (Table 3). The dewlap was usually pulsed once shortly after the sequence of head bobs (Table 3, Figs. 2 and 4), and the duration of each dewlap pulse was quite variable.

In almost half of the displays with seven bobs, an additional dewlap pulse was given during the pause prior to the last head bob (Fig. 2). The duration of this pulse was very short, with only partial extension. "Premature" dewlap pulses of this kind were never observed in the Type A displays of the other sibling species.

Caudalis.—The number of head bobs varied from five to seven, with displays of six head bobs being most common (Fig. 2, labeled sample sizes). This species had a short core display, and many dewlap pulses following the head bob sequence (Table 3, Fig. 4). In at least 85% (N = 119) of the filmed displays, dewlap pulsing was accompanied by a pronounced "tail lift," where the head was raised, the back arched, and the tail raised horizontally. This percentage might be higher, but some filmed sequences were close-ups which excluded the tail region from view. Tail lifts were never observed in the displays of *A. websteri* or *A. brevirostris*.

The *A. caudalis* data provided an opportunity to compare the A displays of conspecific males collected from three geographically separate localities. The Type A display patterns from the three populations were almost identical. Only the duration in the overall core display showed a small difference between populations (Table 4), but correspond-

TABLE 3. Comparison of some descriptive variables for male *A. websteri*, *A. caudalis*, and *A. brevirostris* Type A displays. Means were obtained by first averaging each male's data, then averaging the males' means.

Variable	*websteri*	*caudalis*	*brevirostris*
Bob no. in core display	5	5	5
Mean (+ SE) for core durations (s)	7.28 ± .43 (n = 17)	5.75 ± .15 (n = 17)	6.94 ± .29 (n = 4)
Range in core durations (s)	5.3–10.3	4.7–7.6	6.2–8.3
Mean (+ SE) number of dewlap pulses	1.07 ± .04 (n = 17)	2.15 ± .20 (n = 18)	.02 ± .02 (n = 4)
Tail lift posture	never observed	frequently observed	never observed

TABLE 4. Comparison of some descriptive statistics of Type A displays for male *A. caudalis* collected from three localities, Trou Forban, Source Matelas, and Ile de la Gonave.

Variable	Trou Forban	Source Matelas	Ile de la Gonave
Mean (± SE) for core durations (s)	5.54 ± .15	5.58 ± .57	6.41 ± .28
Range in core duration (s)	4.9–6.4	5.0–6.2	5.7–6.9
CV	9.0	14.5	8.8

ing units maintained almost the same proportions among populations. Because males from these populations shared the same Type A display pattern, the A display data were pooled for this species.

Brevirostris.—The number of head bobs ranged from five to seven, with the displays of six head bobs being most common (Fig. 2, labeled sample sizes). Core duration was intermediate with respect to *A. websteri* and *A. caudalis* (Table 3). Dewlap pulses usually did not follow the head bobbing sequence of the *A. brevirostris* A display (Table 3, Fig. 4).

Type A Display—Interspecific Comparisons

Anolis caudalis showed marked contrasts in its Type A displays as compared with its two neighboring species. The *A. caudalis* core display was significantly shorter than that of the other two species (Wilcoxon 2 sample test, $P \leq 0.01$). In addition, *A. caudalis* pulsed more at the end of its Type A head bobbing sequence than did *A. websteri* and *A. brevirostris* (Wilcoxon 2 sample test, $P \leq 0.0001$), and performed its unique tail lifted during dewlap pulsing.

The relative durations of the units of Type A displays also showed significant interspecific differences. Because there were interspecific differences in core durations, unit durations were expressed as a percentage of the core duration (Fig. 5). The greatest differences were the time proportioned to the first and second head bobs (Units 1 and 3) and to the second interbob pause (Unit 4) between *A. caudalis* and *A. websteri*.

Overall differences between the species Type A displays were evaluated with a stepwise discriminant analysis

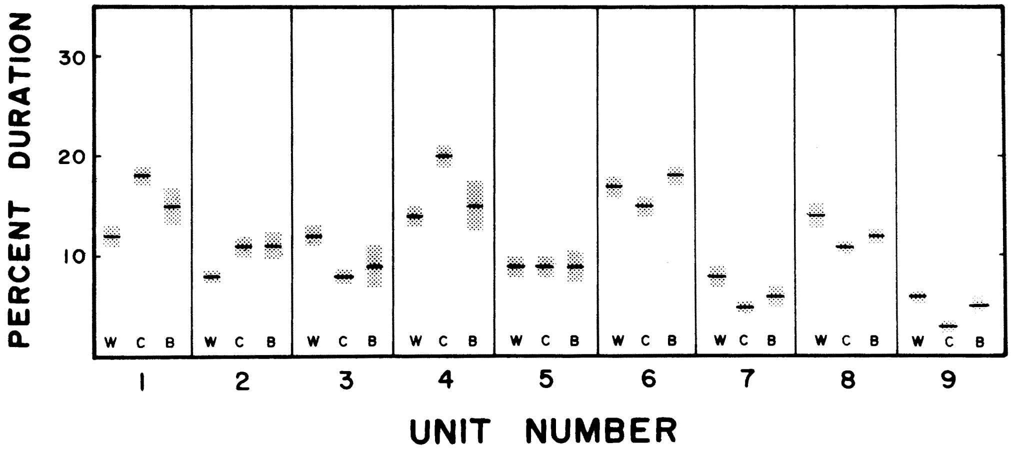

FIG. 5. Unit durations (expressed as a percentage of total core duration) for Type A core displays. Horizontal lines are unit means and bars are 95% confidence intervals for unit durations. For a given unit, the species are arranged from left to right: *A. websteri* (w), *A. caudalis* (c), and *A. brevirostris* (b).

TABLE 5. Summary of the variables entered by the stepwise discriminant analysis program for the Type A displays and their respective F-values to enter, Wilk's lambda values, and approximate F-statistic values.

Step No.	Variable	F-value to enter	Wilk's lambda	Approximate F-statistic
1	Tail lift	230.44	.3633	230.44
2	Unit 3	108.72	.1985	163.00
3	Unit 1	111.91	.1069	179.11
4	Pulse no.	39.54	.0820	162.05
5	Unit 5	15.60	.0731	139.73
6	Unit 9	26.01	.0609	131.29
7	Unit 2	11.06	.0560	118.37
8	Unit 4	17.57	.0493	112.14
9	Bob no.	10.14	.0456	104.28
10	Unit 6	7.70	.0430	97.03
11	Unit 7	24.26	.0361	98.03
12	Unit 8	12.08	.0330	94.68

(Biomedical Computer Programs; Dixon, 1975). Twelve variables were used: the first nine display units (core display), the tail lift posture, the number of dewlap pulses, and the total number of head bobs per display. The variables were entered into the model one at a time until the separation of the A display groups failed to improve significantly. The most important discriminating variables for the Type A displays were tail lift, duration of the first and second head bobs, and number of dewlap pulses (Table 5).

The calculated F-matrix for the A display comparisons contains F values which test the equality of group means for each pair of species groups. All comparisons produced significant F-values ($P \leq 0.001$) (Table 6). The highest F-value was noted for the *A. websteri-A. caudalis* comparison which indicated that these species differed the most in their A display behavior.

The relative distances between the species groups is also reflected on a plot of the display observations and the means for the species groups (Fig. 6). Each species group appears as a separate entity on the discriminant plot with the observations clustered near their respective group means. The first discriminant function, DF-1, which separated the groups along the x-axis, accounted for 86.3% of the total discriminable variance. The second function, DF-2, accounted for the remaining variance. Eigenvalues were 10.42 and 1.66 for DF-1 and DF-2, respectively.

The jacknifed classification procedure, which provided an empirical measure of the success of the discrimination, assigned almost all of the display observations to their original species groups (*A. websteri*—99%; *A. caudalis*—100%; *A. brevirostris*—94%). This procedure used the discriminant scores to assign each observation to the group for which it had the greatest probability of membership. The high percentages of correct classifications confirmed the species uniqueness of the Type A displays.

Hierarchial clustering analysis (SAS; Barr et. al., 1979), designed to group ob-

TABLE 6. F-matrix generated from the stepwise discriminant analysis program using the Type A and B display data and designating the three species as the discriminant groups. The F-values test the equality of group means for each pair of species groups.

Type A	df			*A. brevirostris*	*A. caudalis*
	12, 252	*A. caudalis*		67.25	
		A. websteri		59.82	218.12
Type B	**df**		**Bw_2**	**Bw_1**	**Bc_1**
	8, 123	Bw_1	144.08		
		Bc_1	304.93	218.76	
		Bb_1	63.95	70.55	46.78

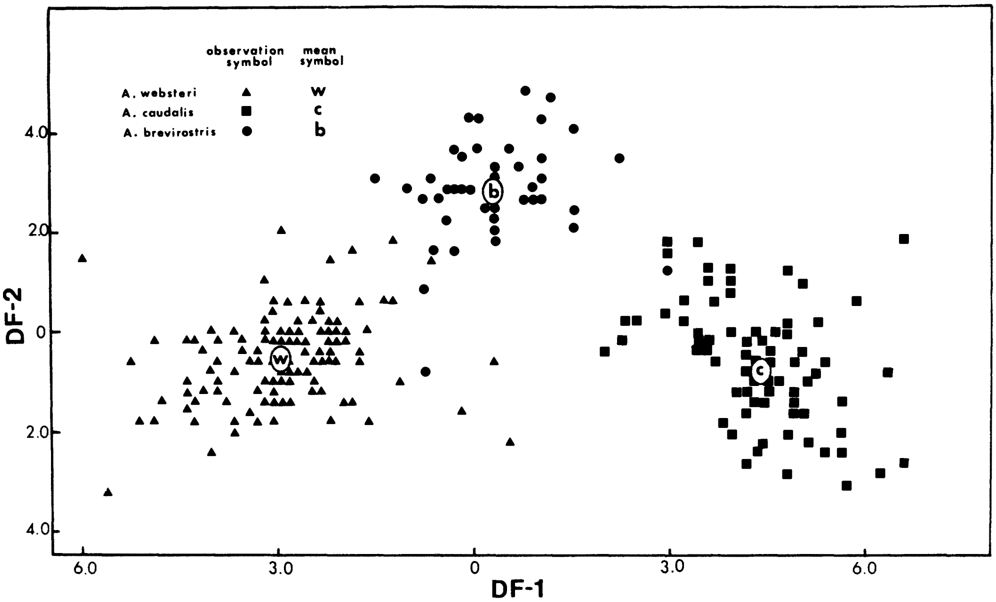

FIG. 6. Individual observations and group means of the discriminant analysis for the Type A displays of *A. websteri, A. caudalis,* and *A. brevirostris* using the standardized discriminant functions (DF-1 and DF-2) as the axes.

servations with similar attributes, demonstrated that the signature displays of *A. websteri* and *A. brevirostris* were the most similar of the three signature display types (Fig. 7). Thus, the A display of *A. caudalis* showed the greatest differences with its two neighboring species.

The A displays of the three species were highly stereotyped. The coefficients of variation (CV = SD/mean × 100) calculated for the unit durations fell below the 35% level (Table 7) typical of ritualized behaviors (Barlow, 1977).

Type B Displays

All three sibling species performed their Type B displays in only male-male and male-female contexts (Table 2). No B displays were given when there was no obvious recipient nearby. The B displays were used along with A displays when males aggressively interacted and as males approached females during courtship.

The siblings' Type B displays had two parts, labeled "Acts." Act 1 contained the first three bobs and their interbob pauses (Units 1–5). After a long pause (interact pause), Act 2 was performed.

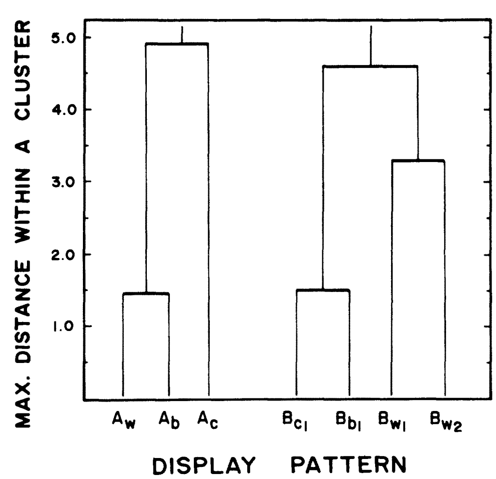

FIG. 7. Phenogram for the Type A displays of *A. websteri* (Aw), *A. caudalis* (Ac), and *A. brevirostris* (Ab), and for Type B displays of *A. websteri* (Bw$_{1-2}$), *A. caudalis* (B$_{c1}$), and *B. brevirostris* (B$_{b1}$).

TABLE 7. Descriptive statistics for unit durations (in seconds) for the Type A displays of *A. websteri* (Aw), *A. caudalis* (Ac), and *A. brevirostris* (Ab).

	Aw				Ac				Ab			
Unit	Mean	SE	95% CI	CV	Mean	SE	95% CI	CV	Mean	SE	95% CI	CV
1	.88	.055	.096	25.7	1.01	.036	.063	14.6	1.07	.074	.174	13.8
2	.61	.029	.050	19.8	.60	.022	.038	15.6	.74	.053	.124	14.3
3	.93	.056	.098	25.1	.46	.017	.030	15.3	.64	.079	.186	24.7
4	.97	.031	.054	13.2	1.15	.030	.052	11.2	1.02	.038	.089	7.5
5	.65	.027	.047	17.2	.54	.021	.036	17.2	.61	.064	.150	21.0
6	1.30	.060	.105	18.9	.89	.036	.062	17.5	1.24	.074	.174	12.0
7	.59	.036	.063	25.3	.34	.021	.036	27.1	.42	.042	.099	20.0
8	1.00	.019	.033	8.0	.68	.033	.057	21.5	.83	.041	.096	9.9
9	.48	.024	.042	21.1	.21	.016	.028	33.0	.33	.025	.059	15.0

Act 2 had three characteristics. First, it was indeterminate (i.e., number of bobs was variable between display performances). Second, the durations of the bobs and interbob pauses produced six different patterns, depending on species. Third, the dewlap was extended regularly and predictably throughout Act 2, but was not a stereotypic component of Act 1; most frequently, it first appeared immediately prior to Act 2 during the interact pause, but in 38% of the B displays it appeared during Act 1.

Act 2 was important for intra- and interspecific comparisons of the B displays. For all siblings, Act 2 consisted of a repeating element. The pattern of the repeating element defined which kind of B display was performed. There were six patterns to the Act 2 elements, hence six kinds of B displays. The repeating elements of four kinds of B displays (B_{c1}, B_{b1}, B_{w1}, and B_{w2}) consisted of two head bobs, the B_{b2} displays had a repeating element of three bobs, and the B_{w3} displays had a repeating element of single bobs.

The four kinds of B displays having two-bob elements could be directly compared, unit for unit. However, the remaining two Type B display patterns, B_{w3} and B_{b2}, had one and three head bobs, respectively, in their Act 2 repeating elements. Therefore, the number of units in their repeating elements differed from the other four B patterns and could not be directly compared. Details of the intra- and interspecific analyses follow.

Websteri.—Anolis websteri males exhibited three kinds of Type B displays. The repeating element of B_{w1} consisted simply of a single bob, that of B_{w2} was composed of double bobs of similar duration, and that of B_{w3} consisted of alternating short and long bobs (Fig. 3). The division of *A. websteri* B displays into three kinds was based primarily on the three distinct temporal patterns of Act 2. However, the temporal pattern of Act 1 also covaried with Act 2 pattern. The jacknifed classification procedure in the discriminant analysis program correctly classified 100% of the B displays into the three Act 2 categories when only the unit variables of Act 1 were provided for analysis. Thus, the pattern present in Act 1 predicted which of the three patterns would be present in Act 2 of the display.

Caudalis.—Anolis caudalis males exhibited only one Type B pattern (B_{c1}) (Fig. 3). Act 2 consisted of alternating long and short head bobs.

Brevirostris.—Anolis brevirostris males exhibited two kinds of Type B displays, B_{b1} and B_{b2}. The repeating element of B_{b1} was a long bob followed by a short bob, and that of B_{b2} consisted of a long bob followed by two shorter bobs of similar duration (Fig. 3). The division of *A. bre-*

TABLE 8. Summary of the variables entered by the stepwise discriminant analysis program for the Type B displays and their respective *F*-values to enter, Wilk's lambda values, and approximate *F*-statistic values.

Step no.	Variable	*F*-value to enter	Wilk's lambda	Approximate *F*-statistic
1	Unit 5	356.33	.1084	356.33
2	Unit 12	91.84	.0346	188.25
3	Unit 4	94.34	.0108	188.23
4	Unit 11	45.90	.0052	177.04
5	Unit 10	18.50	.0036	155.26
6	Unit 3	11.81	.0028	137.60
7	Unit 13	7.03	.0024	122.04
8	Unit 1	5.69	.0021	109.95

virostris displays into two kinds was based primarily on the temporal pattern observed in Act 2 of the displays. The jackknifed classification procedure also showed that the Act 1 pattern covaried with the Act 2 patterns for the two kinds of B displays. When given only Act 1 variables for the analysis, 100% correct classification resulted. Thus, the pattern of Act 1 predicted which of the two bob patterns would appear in the repeating elements of Act 2.

Type B Display—Interspecific Comparisons

B_{w1}, B_{w2}, B_{c1}, and B_{b1} were chosen for discriminant analysis because their units were directly comparable. Of the thirteen display units provided for the analysis, eight were selected by the stepwise method to be discriminant variables. All discriminant variables produced highly significant *F*-values ($P \leq 0.001$) (Table 8). For paired group comparisons, the B_{w2}-B_{c1} comparison produced the highest *F*-value, being the most different; the B_{c1}-B_{b1} comparison resulted in the lowest *F*-value, being most similar (Table 6). As with the A display types, the greatest degree of difference was noted between *A. websteri* and *A. caudalis*, whereas the smallest degree of difference was noted between *A. caudalis* and *A. brevirostris*.

The three discriminant functions, DF-1, DF-2, and DF-3, accounted for 70.1, 27.2, and 2.7% of the total variance, respectively. Eigenvalues for DF-1, DF-2, and DF-3 were 23.60, 9.15, and .91, respectively. On the discriminant plot, each B display group was fairly distinct; the display observations clustered about the mean of their respective species groups without much overlap (Fig. 8).

High percentages of correct classifications were obtained for each display type; all were 100%, except for 90% for B_{b1}. Thus, even those display types which most closely resembled one another exhibited consistent differences in the temporal patterning of the head bobs and interbob pauses.

The relationships of the above four Type B display patterns were addressed with hierarchial clustering analysis. B_{c1} and B_{b1} showed the strongest similarities (Fig. 7).

Type B displays were also quite stereotyped. Most units had coefficient of variation values which fell below the 35% criterion level (Barlow, 1977) for stereotypic behaviors (Table 9).

DISCUSSION

The "brevirostris" species possess multiple head bob display repertoires, each containing a Type A pattern and one to three kinds of Type B patterns. The Type A display appears in all contexts (Table 2). It is the only head bob display used in non-directed displaying, the context which defines this pattern as the species "signature" display (Jenssen, 1977). The signature display is considered a species' basic head bob pattern, functioning in non-directed advertisement, species identification, mate selection, and territorial defense.

The Type B displays were performed only in male-male and male-female interactions. This last context is unusual. In other anoles with multiple display repertoires (e.g., *A. limifrons*, Hover and Jenssen, 1976; *A. townsendi*, Jenssen and Rothblum, 1977), just the signature dis-

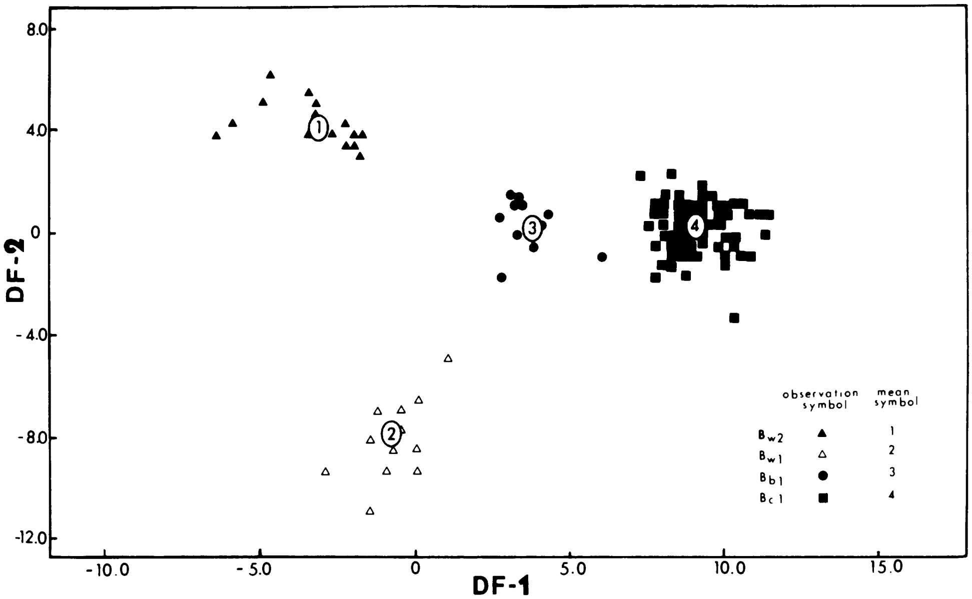

FIG. 8. Individual observations and group means of the discriminant analysis for the Type B displays of *A. websteri* (B_{w1-2}), *A. caudalis* (B_{c1}), and *A. brevirostris* (B_{b1}) using the standardized discriminant functions (DF-1 and DF-2) as the axes.

play is used when courting; the nonsignature displays are restricted to territorial defense (male-male context). The "brevirostris" species, however, frequently used their Type B displays during courtship as well as in male-male encounters (Table 2). It is unlikely that males are agonistically oriented toward females. More likely the Type B display function has been split between the expected aggressive signal and a more recently derived role as an additional "species recognition-female attraction" signal. This latter function may not only reinforce that of the signature display, but may possibly be more effective because of the large number of dewlap pulses flashed throughout the Type B displays.

Experimental evidence indicates that the species-unique head bobbing displays function to attract conspecific females (Jenssen, 1970), and that dewlap color (Crews and Williams, 1977; Rand and Williams, 1970; Williams and Rand, 1977) and movement (Crews, 1975, 1978) may in themselves be important in female mate selection. Thus any species-unique differences among the sibling "brevirostris" displays may be involved in a behavioral isolating mechanism. Our analysis has shown that even though the three sibling species have similar A and B displays, there are definite species-defining differences. Though our data are descriptive in nature, they suggest that the display behavior is a likely candidate as an isolation mechanism among the "brevirostris" siblings.

Inferential evidence for the above interpretation comes from interspecific comparisons of display characteristics at localities where the species interface. The first character is dewlap color. Webster and Burns (1973) noted that at the websteri-caudalis interface, dewlap color is bright orange in *A. websteri* and white in *A. caudalis*. At the caudalis-brevirostris interface it is bright orange in *A. caudalis* and variably colored, but pale in *A. brevirostris*. A second character is

TABLE 9. Descriptive statistics for unit durations (in seconds) for the Type B displays of *A. websteri* (B_{w1}, B_{w2}, B_{w3}), *A. caudalis* (B_{c1}), and *A. brevirostris* (B_{b1}, B_{b2}).

	B_{w1}				B_{w2}			
Unit	Mean	SE	95% CI	CV	Mean	SE	95% CI	CV
1								
2	.61	.057	.113	25.1	.04	.016	.029	130.1
3	.45	.021	.040	13.2	.28	.027	.048	33.2
4	.29	.019	.036	18.4	.73	.029	.052	14.5
5	.89	.030	.057	9.6	.89	.029	.052	11.8
6	1.28	.050	.095	11.1	1.19	.050	.089	15.0
7	.40	.036	.067	26.4	.48	.016	.029	12.0
8	.92	.057	.106	8.6	.09	.018	.032	72.3
9	.70	.024	.045	10.2	.52	.028	.050	19.4
10	.77	.018	.033	7.1	.71	.025	.044	12.7
11	.26	.019	.035	22.3	.31	.011	.020	13.5
12	.91	.126	.234	41.4	.06	.013	.024	75.8
13	.61	.025	.047	12.1	.40	.018	.033	16.5

	B_{w3}				B_{c1}			
Unit	Mean	SE	95% CI	CV	Mean	SE	95% CI	CV
1	.53	.075	.176	31.7	.21	.020	.034	45.3
2	.03	.013	.027	129.2	.21	.020	.034	45.3
3	.21	.020	.044	52.2	.80	.034	.058	11.4
4	1.45	.176	.375	21.8	.56	.019	.033	21.1
5	.74	.090	.192	27.2	.28	.013	.023	22.9
6	1.45	.099	.212	15.4	1.15	.054	.093	22.5
7	.68	.036	.077	11.8	1.23	.033	.056	13.1
8	1.16	.074	.149	15.6	.40	.032	.054	38.7
9	.64	.077	.154	29.2	.21	.008	.013	17.8
10	.89	.045	.091	12.5	.43	.014	.024	16.1
11	.53	.055	.110	25.4	.99	.022	.039	11.1
12	.77	.048	.097	15.4	.30	.024	.041	37.9
13	.47	.044	.090	23.1	.17	.007	.011	18.4
14	.65	.053	.108	20.1				
15	.40	.035	.071	21.4				

	B_{b1}				B_{b2}			
Unit	Mean	SE	95% CI	CV	Mean	SE	95% CI	CV
1	.41	.073	.171	35.7	.41	.057	.134	28.2
2	.27	.070	.165	52.3	.67	.055	.129	16.3
3	.40	.050	.118	25.0	.35	.023	.054	13.3
4	.73	.039	.092	10.8	.48	.035	.082	14.4
5	.50	.028	.066	11.4	.36	.015	.035	8.4
6	1.46	.059	.139	8.1	1.59	.030	.071	3.8
7	.77	.044	.104	11.4	.72	.046	.108	12.8
8	.55	.040	.094	14.5	.68	.030	.071	8.7
9	.32	.011	.026	6.9	.28	.017	.040	12.0
10	.81	.040	.094	9.9	.36	.019	.045	10.7
11	.65	.045	.106	13.7	.29	.019	.045	13.4
12	.43	.030	.071	14.2	1.00	.022	.052	4.5
13	.26	.014	.033	11.1	.67	.027	.064	8.0
14					.63	.017	.040	5.2
15					.28	.006	.014	4.4
16					.32	.022	.052	13.5
17					.25	.010	.024	8.0

dewlap movement. *Anolis caudalis* shows the greatest contrast with each of its two neighboring species by having the most dewlap pulses following its signature display. These pulses are accentuated by a marked head rise and the tail lift posture unique to *A. caudalis*. The last character is head bob cadence. The greatest differences for both A and B display patterns occurred between *A. websteri* and *A. caudalis* (Tables 6 and 11). It is just south of Montrouis where both of these species abut at high population densities. The signature display of *A. caudalis* is also most distinct from *A. brevirostris* (Fig. 7). The only exception where *A. websteri* and *A. brevirostris* comparisons showed greater differences than those involving *A. caudalis* were for the caudalis-brevirostris Type B display cadence. However, this is somewhat misleading because we restricted the comparison to only those B displays having a repeating two-bob element. In fact, *A. brevirostris* has a second B pattern based on a repeating three-bob element which is quite distinct from the single caudalis B display.

In summary, the display characteristics were most divergent when comparing adjacent species than when comparing non-contiguous species. These differences were most pronounced at the websteri-caudalis boundary where contact is intense. We suggest that these differences in display features represent character displacement and have occurred through sexual selection for species recognition.

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Literature Cited

Arnold, D. L. 1980. Geographic variation in *Anolis brevirostris* (Sauria: Iguanidae) in Hispaniola. Breviora 461:1–31.

Barr, A. J., J. H. Goodnight, J. P. Sall, W. H. Blair, and D. M. Chilko. 1979. SAS User's Guide, 1979 edition. SAS Instit. Inc., Raleigh, North Carolina.

Barlow, G. W. 1977. Modal Action Patterns, pp. 100–105. *In* T. A. Sebeok (ed.), How Animals Communicate. Indiana Univ. Press, Bloomington.

Crews, D. P. 1975. Effects of different components of male courtship on environmentally-induced ovarian recrudescence and mating preferences in the lizard, *Anolis carolinensis*. Anim. Behav. 23:349–356.

———. 1978. Integration of internal and external stimuli in the regulation of lizard reproduction, pp. 149–171. *In* N. Greenberg and P. MacLean (eds.), Behavior and neurology of lizards: an interdisciplinary colloquium. N.I.M.H., Rockville, Maryland.

———, and E. E. Williams. 1977. Hormones, reproductive behavior, and speciation. Amer. Zool. 17:261–270.

Dixon, W. J. (ed.). 1975. Biomedical computer programs. Univ. California Press, Los Angeles.

Hover, E. L., and T. A. Jenssen. 1976. Descriptive analysis of agonistic displays of *Anolis limifrons* (Sauria: Iguanidae). Behaviour 58:173–191.

Jenssen, T. A. 1970. Female response to filmed displays of *Anolis nebulosus* (Sauria, Iguanidae). Anim. Behav. 18:640–647.

———. 1977. Evolution of anoline lizard display behavior. Amer. Zool. 17:203–216.

———, and E. L. Hover. 1976. Display analysis of the signature display of *Anolis limifrons* (Sauria, Iguanidae). Behaviour 57:227–240.

———, and L. Rothblum. 1977. Display repertoire analysis of *Anolis townsendi* (Sauria: Iguanidae) from Cocos Island. Copeia 1977:103–109.

Rand, A. S., and E. E. Williams. 1970. An estimation of redundancy and information content of anole dewlaps. Amer. Nat. 104:99–103.

Webster, T. P., and J. M. Burns. 1973. Dewlap color variation and electrophoretically detected sibling species in a Haitian lizard, *Anolis brevirostris*. Evolution 27:368–377.

Williams, E. E., and A. S. Rand. 1977. Species recognition, dewlap function, and faunal size. Amer. Zool. 17:261–270.

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