A Comparative Display Analysis of Three Sibling Species of _Anolis_ Lizards from Hispaniola

by

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(ABSTRACT)

The display repertoires of three sibling species of *Anolis* lizards, were quantitatively analyzed and described. These species are distributed along Haiti's western coast with no major geographic barriers separating their populations. *Anolis websteri* is the northernmost species, *Anolis caudalis* is centrally located, and *Anolis brevirostris* is the southernmost species. Except for contrasting dewlap color at the species contact zones, they are identical in physical appearance.

Behavioral mechanisms have been implicated in the reproductive isolation of the species. Because the head bob displays consistently incorporate the dewlap and are important in anoline communication, they may be the focal point of this isolation. This study documents a species-unique display repertoire for each of the siblings and

thereby supports this hypothesis. Analysis of 736 head bob displays revealed that each species possesses one stereotyped Type A display and one to three stereotyped B displays (*A. caudalis*, one; *A. brevirostris*, two; *A. websteri*, three). Each species' A display resembled that of its siblings, however, discriminant analysis procedure clearly discriminated between the three species' A displays. This procedure also demonstrated differences between the Type B displays.

The six kinds of Type B displays in the combined repertoires were considered derived from one B display pattern. An interpretation of the evolutionary sequence of these patterns is provided in a cladogram in which the *A. caudalis* display was considered the outgroup. The cladogram shows the three displays of *A. websteri* are the most apomorphic and the two displays of *A. brevirostris* the most plesiomorphic.

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INTRODUCTION

The Hispaniolan lizard, Anolis brevirostris, has recently been found to represent at least three sibling species (Webster and Burns, 1973). The three species are contiguously distributed along Haiti's western coast with no major geographic barriers separating their populations. Webster and Burns (1973) suggested that a reproductive isolating mechanism may prevent genetic exchange between adjacent gene pools. A behavioral mechanism is probable as the color of the dewlap, a structure used in social communication, is a distinguishing morphological feature of the three species.

The present study is a first step in evaluating the hypothesis that a behavioral isolating mechanism is operating within the species complex. The objectives are to: (1) make a quantitative analysis of each species' display repertoire, (2) compare these repertoires for consistent, species-unique features which might serve in species recognition and mate selection, and (3) infer the evolutionary relationships of the species' display repertoires.

METHODS AND MATERIALS

SUBJECTS

The three sibling species are relatively small, stocky anoles (males $\leq$ 51mm SVL, females $\leq$ 47mm 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 structural 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 low and often dense *Acacia* shrub (Arnold, 1980).

The three anoline species recognized by 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.

Dewlap color appears to be the most diagnostic external character among the siblings. In areas immediately adjacent to interfaces between two species, species have markedly contrasting dewlap coloration. *Anolis websteri* dewlaps are uniformly orange or orange with a narrow yellow margin. Dewlap color in *A. caudalis* is pale white or yellow sometimes with a small orange basal spot at the *A.websteri-A.caudalis* interface, but is 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, T. A. Jenssen (personal communication) found *A. caudalis* dewlaps ranging from white to orange and characterized by a white margin within one kilometer of *A. websteri*. Dewlap color in *A. caudalis* at the *A. caudalis-A. brevirostris* interface is bright orange. In contrast, *A. brevirostris* dewlaps are monochromatic in pale shades of orange, peach, yellow, gray, olive, and brown (Arnold, 1980).

COLLECTIONS

The display analysis of the sibling species was based on three collections. The first was collected and sent to the V.P.I. & S.U. 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 by T. A.

Jenssen; the 1977 collection also included specimens from Ile de la Gonave. During a combined period of three months in 1975 and 1977, extensive field notes and films were made by T. A. Jenssen on social behavior of A. websteri and A. caudalis in and around the contact zone. The filming in the field as well as the lab was done by a super-8 camera set at 18 frames/s.

LABORATORY PROTOCOL

In the laboratory lizards were toe clipped for permanent identification and were housed in glass-fronted wooden enclosures which measured 1.2 x 0.6 x 0.7m. 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. Occasional field sweepings supplimented this diet. Water was sprayed onto the foilage daily as well as being available in shallow dishes.

Displays were recorded on cinema film. 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 heat for lizard thermoregulation. Initially, the subject shared the enclosure with several females; this situation produced non-directed and male-female behavior. After a sufficient sample of displays had been filmed within these contexts, another male was introduced to elicit displays within a male-male context.

FIELD PROTOCOL

In the field, 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 was also filmed. In this way it was possible to identify many of the social contexts within which displays were performed. If context was uncertain during film analysis, it was recorded as unknown.

FILM ANALYSIS

Filmed displays were viewed frame-by-frame with a Kodak MFS-8 movie projector (Jenssen and Hover 1976). Display-action-pattern (DAP) graphs were constructed to provide visual representations of the displays. In each DAP graph, head amplitude and dewlap extensions were plotted on the y-axis and duration on the x-axis.

During preliminary analysis of the DAP graphs, it was apparent that the displays within each species' repertoire fell into one of two categories. The first category was composed of very stereotyped, species-unique display patterns which were labeled the "Type A" displays (Fig. 2). Displays of the second category were much different from the Type A displays and were labeled the "Type B" displays. Each species performed one to three pattern variations of the Type B display (Fig. 3).

A total of 736 laboratory and field filmed displays by males was analyzed (Table 1). Each display was divided into "units". Each unit encompassed the duration of either a head bob or an interbob pause. 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 unit duration of each unit was determined by counting the number of cinema frames which composed each bob and interbob pause. Each frame represented .056s (18 frames/s). The Type A displays that were initially analyzed and for all of the more complex Type B displays, DAP graphs were made to insure pattern identification, and unit durations were taken from the DAP graphs. Unit durations for each remaining Type A display were taken directly from the films.

The predictable patterns of head and dewlap movement common to each performance of a display type comprise its "core". The core of each species' Type A display included the first five head head bobs and interbob pauses (units 1 through 9). When the durations of the first nine units of the display were totaled, the core duration was obtained.

A cladogram was constructed using the Type B displays. In this analysis the B display of *A. caudalis*, Bc1, was considered the most primitive and was used as an outgroup for purposes of establishing character polarity. A species B display unit was considered plesiomorphic (primitive) when its mean duration fell within a $\pm$ 66% of the corresponding Bc1 unit mean. If a species display unit was longer or shorter than the Bc1 mean it was considered apomorphic (derived). Both longer and shorter apomorphic states were considered in the analysis, but one state was not necessarily considered to be more derived than the other.

The following variables were recorded for each display: (1) lizard ID; (2) collection site; (3) display type; (4) field or lab filmed; (5) unit durations; (6) social context; and(7) concomitant display modifiers. The last variable involved optional postures (static modifiers) or movements (dynamic modifiers) which sometimes accompanied the core display (Tables 2 and 3) (see also Jenssen, 1977, 1978, 1979). Quantitative analysis of the display variables was then carried out with the Statistical Analysis System (Barr et al., 1976, 1979) and Biomedical Computer Programs (Dixon, 1975).

RESULTS

DISPLAY REPERTOIRES

The display repertoires of _Anolis websteri_, _A. caudalis_, and _A. brevirostris_ were similar. All three species had Type A displays which resembled one another, while possessing more subtle characteristics that were distinctly species-unique (Fig. 2). From contextual information, the Type A displays were the only displays performed in non-directed situations (Table 4).

The Type B displays were also found in the repetoires of all three sibling species. They were similar between the species; however, they also had species-unique features as well (Fig. 3). _Anolis websteri_ had three variations of the Type B display, _A. brevirostris_ had two, and _A. caudalis_ only one.

TYPE A DISPLAYS

Websteri. The number of head bobs varied from five to seven, with displays of six head bobs being most common (Fig. 4). The core display of _A. websteri_ was the longest of the three species (Table 5).

Anolis websteri males typically pulsed the dewlap once shortly after the sequence of head bobs (Table 5, Figs. 2 and 5). The duration of the dewlap pulse varied between displays, but the dewlap was almost always fully extended prior to retraction.

In almost half (n=83) of the displays with seven bobs an additional dewlap pulse was given during the pause prior to the last head bob (unit 12) (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. 4). This species has a shorter core display thaneither *A. websteri* or *A. brevirostris* (Table 5).

Of the three species *Anolis caudalis* males pulsed the dewlap most frequently after head bobbing sequence (Table 5) and pulses were variable in number (Fig. 5). They usually raised their heads and arched their backs slightly during dewlap pulsing. A tail lift occurred with the dewlap pulsing in 72.3 % (n=119) of the displays for which the tail was visible. Tail lifts were never observed in the Type A displays of *A. websteri* or *A. brevirostris*.

The *A. caudalis* data provided an opportunity to compare the signature displays of conspecific males collected from three geographically separate localities (Table 6). To permit the interpopulational comparison of the temporal patterning of head bobs and pauses, each unit duration was expressed as a percentage of the core duration. Because all males shared the same Type A display pattern (Fig. 6), the data for Type A displays 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. 4). Core duration was intermediate with respect to A. websteri and A. caudalis (Table 5).

Unlike the other two species, dewlap pulses usually did not follow the head bobbing sequence of the A. brevirostris A display (Table 5, Fig. 5). A single dewlap extension was observed in two of the 22 displays performed by one male. The other males did not pulse the dewlap during their display performances.

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 other two species (Wilcoxon 2 sample test, $p \leq .01$). 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, $p \leq .0001$) (Table 5).

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. 7). 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 stepwise discriminant analysis (Biomedical Computer Programs; Dixon, 1975). The twelve variables used were the first nine display units, the tail lift modifier, 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 sequence of variables entered was based on a variable's F value in a one-way analysis of variance between the species' Type A displays (_e.g._, the first variable entered had the highest F value and was the best discriminating variable). All variables included in the final model produced highly significant F values ($p \leq .001$) (Table 7). 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 7).

At each step a Wilk's lambda or U-statistic was computed. This multivariate statistic tested the equality of group means for those variables in the model. Each

Wilk's lambda value was transformed to an approximate F-statistic which was comparable with the F distribution. The A display groups have different groups means as shown by the the highly significant ($p \leq .001$) F-value produced after all the variables had been entered into the model (Table 7).

The F-matrix contains F values which tested the equality of group means for each pair of A display groups. All comparisons produced significant F-values ($p \leq .001$) (Table 8). 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 groups is also reflected on a plot of the display observations and the group means (Fig. 8). Each 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 (Table 9).

The jackknified classification procedure, which provided an empirical measure of the success of the discrimination, assigned almost all of the display observations to their original groups (Table 10). 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 that Type A display differences did exist and that the variables selected by the stepwise method exhibited these differences.

Hierarchial clustering analysis (SAS; Barr et. al., 1977), designed to group observations with similar attributes, was used to describe the Type A display relationships. The signature displays of A. websteri and A. brevirostris were selected as being the most similar of the three signature display types (Fig. 9).

Lizards of all three species gave displays with variable numbers of head bobs. They performed displays of either five and six, six and seven, or five, six, and seven head bobs. To examine whether the unit durations in displays of lower numbers of head bobs were different from those in displays of higher numbers of head bobs, Spearman's rank correlation analysis was used. No significant correlations were obtained for the A. brevirostris Type A displays, but for A. websteri and A. caudalis the durations of several head bobs in the core display increased in displays of higher numbers of displays (Table 11).

The signature displays of the three species were highly stereotyped. The coefficients of variation (Mean/S.D * 100) calculated for the unit durations fell below the 35 % level

(Table 12) typical of ritualized behaviors (Barlow, 1977).

TYPE B DISPLAYS

The Type B displays had two parts labeled "Acts". Act1 contained the first three bobs and their interbob pauses (Units 1 through 5). The units of Act1 in each Type B display pattern were considered to be homologous. After a long pause (interact pause), Act2 was performed. Act2 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 one to three patterns, depending on the species. Third, the dewlap was extended regularly throughout Act2, but was not a stereotypic component of Act1; it most frequently first appeared immediately prior to Act2 during the interact pause (Fig. 10).

Homologous head bobs for the Type B displays were identified by visual inspection of the DAP graphs. Act2 of each Type B DAP graph consisted of repeating elements of one to three head bobs. Head bobs were qualitatively described based on the number and duration of bobs in the repeating elements (Table 13). The repeating elements of four (Bc1, Bb1, Bw1, and Bw2,) of the six Type B display patterns consisted of two head bobs. These were considered to be homologous (Fig. 11). The remaining two Type B display patterns, Bw3 and Bb2, had one and three head bobs, respectively, in their Act2 repeating elements. These displays were not considered to be homologous with the other four display patterns.

Websteri. *Anolis websteri* males exhibited three kinds of Type B displays (Bw1, Bw2, and Bw3) (Fig. 3).

The division of *A. websteri* B displays into three types was based primarily on the three distinct temporal patterns of Act2. However, the temporal pattern of Act1 also differed for each B display according to the results of the jackknifed classificationprocedure in the discriminant analysisprogram. procedure. Only the unit variables of Act1 were provided for this analysis, yet 100% correct classification was obtained for each Type B display group. Thus, the pattern present in Act1 predicted which of the three patterns would be present in Act2 of the display.

The three *A.websteri* Type B displays appeared in both the male-male and male-female contexts. Thus, it did not appear that they served different functions. However, there was a tendency for the number of static modifiers that accompanied the B displays to vary according to which B pattern was performed. Males performing Bw1 and Bw2 displays employed a relatively low number of static modifiers, whereas more were used by males performing Bw3 displays (Fig. 12). In addition, males using only their forelimbs primarily performed Bw2 and Bw3 displays, whereas those employing all four limbs mostly performed the Bw3 displays (Fig. 13). Because increasing numbers of modifiers tend to indicate increasing arousal (Jenssen, 1977), a male may shift between the three B patterns as he becomes more aroused.

The typical Act2 pattern characteristic of Bw1 and Bw2. displays sometimes shifted to one consisting of single head bobs. In 27 % (N=26) of the Bw1 and 75 % (N=52) of the Bw2 displays the first bob in the repeating element decreased in duration and amplitude until there were only single head bobs. The point of pattern transition was variable, but most Bw1 and Bw2 performances continued through the fourth head bob of Act2. The deletion of the first head bob in the Act2 repeating segment of Bw1 and Bw2 indicated that the second head bob in each of these display types might be homologous to each single head bob in Act2 of Bw3 (Fig. 11).

Caudalis. *Anolis caudalis* males exhibited only one Type B pattern (Bc1) (Fig. 3). Act2 consisted of alternating long and short head bobs. However, the "long-short" bob pattern shifted to single head bobs in 12 % of the displays, a phenomenon also observed in Bw1 and Bw2 displays.

The majority of Bc1 displays were accompanied by a relatively low number of static modifiers and the majority were performed using all four limbs (Figs. 12 and 13).

Brevirostris. Anolis brevirostris males exhibited two kinds of Type B displays (Bb1 and Bb2) (Fig. 3). The division of A. brevirostris displays into two kinds was based primarily on the temporal pattern observed in Act2 of the displays. The jackknifed classification procedure was used to show that Bb1 and Bb2 differed in the patterning of Act1. Only Act1 variables were provided for the analysis, but 100% correct classification results were obtained for the two Type B display groups. Thus, the pattern of Act1 predicted which pattern, "long-short" or "long-short-short" will appear in Act2 of the display.

The function of the two Type B displays was not clear; Bb1 and Bb2 displays were observed in both male-male and male-female contexts. The relatively high numbers of static modifiers associated with most Bb2 performances possibly indicates that males were more highly aroused during Bb2 performances (Fig. 12). Both Bb1 and Bb2 displays were most frequently performed using all four limbs (Fig. 13).

TYPE B DISPLAY INTERSPECIFIC COMPARISONS

Bw1, Bw2, Bc1, and Bb1 were chosen for discriminant analysis because their units were considered homologous and therefore 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 ($p \leq .001$) (Table 14). For paired group comparisons, the Bw2-Bc1 comparison produced the highest F-value; the Bc1-Bb1 comparison resulted in the lowest F-value (Table 15). 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 percent of the total variance, respectively (Table 16). On the discriminant plot, each B display group was fairly distinct; the display observations clustered about their respective group means without much overlap (Fig. 14).

High percentages of correct classifications were obtained for each display type (Table 17). 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 heirarchial clustering analysis. Bc1 and Bb1 showed the strongest similarities (Fig. 15).

The cladogram shows that the A. brevirostris B displays, Bb1 and Bb2, have more plesiomorphic characters than do the _A_. _websteri_ B displays, Bw1, Bw2, and Bw3 (Fig. 16). Only two automorphies distinguish Bb1 from the most primitive display, Bc1, but five synapomorphies unite Bb2 with the Bw1-3 displays. Bw1 and Bw3 have 3 synapomorphies; whereas both are united with Bw2 by only two synapomorphies. The cladogram requires 16 steps, compared with the theoretical minimun number of 13.

Type B displays were also stereotyped behaviors. Most units had C.V.'s which fell below the 35 % criterion level (Barlow, 1977) for relative stereotypy (Table 18).

DISCUSSION

ISOLATING MECHANISM

Type A displays serve as the signature display for each species. The signature display is considered the basic communication pattern used for non-directed advertisement, species identification, mate attraction, and territorial defense. The Type A displays were the only displays that were not always directed toward another male or female. In species having multiple displays repertoires, it is this non-directed context which defines which display pattern serves as the "signature display" (*sensu* Jenssen, 1977)

Experimental evidence suggests that anoline head bobbing serves as a species recognition signal used in mate selection. *Anolis nebulosus* females shown a film loop of a male signature display and a film loop of altered versions of the display were differentially attracted to the normal display (Jenssen, 1971). Moreover, the signature display is the sole display type used during the courtship of anoles having multiple display repertoires (*e.g.* Hover and Jenssen, 1976; Jenssen and Rothblum, 1977).

Each "brevirostris" species possesses a multiple display repertoire consisting of one signature (Type A) display and one to three Type B displays. Webster and Burns

(1973) hypothesized that these communication signals may be acting as a reproductive isolating mechanism within the "brevirostris" complex. Although non-experimental in nature, the present study lends support to their hypothesis.

In previously studied anoles with multiple display repertoires (e.g., A. limifrons, Hover and Jenssen, 1976; A. townsendi, Jenssen and Rothblum, 1977), the non-signature display patterns are restricted to male-male territorial aggression. With the "brevirostris" sibling species, however, the Type B displays were used during courtship as well as in the context of male-male interactions (Table 4). It is unlikely that males are agonistically oriented toward females. More likely the Type B display function has split, with the more recently derived role serving as an additional "species recognition-female attraction" signal. This latter function may reinforce with 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.

The stereotyped head bobbing displays of most anoline species incorporate the dewlap. Dewlap color (Rand and Williams, 1970) and movement (Crews, 1970) may in themselves be important in female mate selection. Dewlap color and movement have diverged among the three sibling species, possibly as a result of character displacement. Where the distributions of the species interface, the species possess contrasting dewlap colors and dewlap movement. In the north, _A_. _websteri_ and, to a greater extent, _A_. _caudalis_ perform dewlap pulses at the conclusions of their signature displays. Males of the latter species not only perform the most numerous pulses, but also accentuate the pulses with a marked head rise and concomitant tail lift. At least near Montrouis, this _A_. _websteri_-_A_. _caudalis_ contact zone is intimate and involves high population densities of both species. In contrast, the _A_. _caudalis_-_A_. _brevirostris_ interface in the south is less obvious due to an apparent decrease in preferred habitat along the potential line of contact. Nevertheless, dewlap use in the signature displays differs here also; _A_. _brevirostris_ males almost never give dewlap pulses and _A_. _caudalis_ males usually give two or more dewlap pulses. This interspecific difference may be interpreted as a character divergence on the part of _A_. _brevirostris_ (see Williams and Rand, 1977:266), or it may be due to less selection pressure to exhibit dewlap color because of less frequent contact of _A_. _brevirostris_ with _A_. _caudalis_. Dewlap color and movement seem a redundant aspect of species-unique head bobbing patterns. However, in an area of high probability of sibling species contact such as the _A_. _websteri_-_A_._caudalis_ contact zone, dewlap color and movement might be reinforced in order to enhance species discrimination.

BREVIROSTRIS-DISTICHUS HYPOTHESIS

One suspected impetus for speciation within the "brevirostris" complex is a closely related and ecologically similar species, *Anolis distichus* (Webster and Burns, 1973; Crews and Williams, 1977). *Anolis websteri* and *A. brevirostris* are sympatric and syntopic with *A. distichus*, whereas *A. caudalis* is not. Thus, character displacement may have affected the species recognition signals in the ancestral *A. websteri* and *A. brevirostris* populations to reduce the occurrence of "brevirostris"-"distichus" hybridization, an event which occurs on occasion (Webster, 1978). With divergence occurring in the courtship signals of the northern and southern ancestral "brevirostris" populations, gene flow with the central populations of the species would have been disrupted. Dewlap color was thought to be the primary character that underwent divergence (Webster and Burns, 1973).

However, *A. distichus* has a large display repertoire (Fig. 17) and every bob pattern is distinct from the bob patterns of the three "brevirostris" species (Jenssen, 1982). Because of their different display repertoires, it seems improbable that ancestral "brevirostris" and "distichus" could have misidentified one another. However, this does not rule out the possibility that dewlap color underwent divergence in the ancestral *A. websteri* and *A. brevirostris* populations therefore providing at least one additional species recognition signal. Rand and Williams (1970) argue that species recognition in complex faunas is not based on a single stimulus but on a complex of redundant stimuli.

EVOLUTIONARY SEQUENCE

Most non-anoline iguanid lizards exhibit only one display type (*sensu* Jenssen, 1977). One exception is *Phenacosaurus heterodermus* that exhibits two types of displays in its repertoire (Jenssen, 1975). Because the phenacosaurs are thought to have diverged early from the primitive mainland stock of the *Anolis* alpha section (Etheridge, 1960), multiple repertoires may have been an early development in the evolution of display behavior in *Anolis* (Jenssen, 1975).

Thus, it is difficult to determine the number of display types in the *Anolis* repertoire. First, the display repertoires of most *Anolis* are unknown. Second, those that are known exhibit dramatic differences in number of display types. For example, *A. nebulosus* exhibits only a single type of display (Jenssen, 1971) whereas *A. limifrons* exhibits five types of displays (Hover and Jenssen, 1976).

The non-signature or agonistic displays of the latter species are thought to have evolved from the signature display because the five display patterns are similar (Jenssen, 1978).

The B displays of the "brevirostris" sibling species show strong intra and interspecific similarities. For this reason I consider the multiple B display patterns derived from a single B pattern. As _A_. _caudalis_ has only one B display, I consider this simple condition the most primitive for the "brevirostris" species group. This makes Bc1 the outgroup display for the cladistic analysis.

The results obtained from the phenogram (Fig. 15) and the cladogram (Fig. 16) agree with one another. The phenogram clustered the _A_. _brevirostris_ Bb1 display with the _A_. _caudalis_ Bc1 display indicating that these two show the strongest overall similarities. The cladogram shows that Bb1 is the most primitive display in the combined repertoires of _A_. _websteri_ and _A_. _brevirostris_ when Bc1 is used as a standard. In contrast, the _A_. _websteri_ B displays are the most highly derived of those in the species complex. Thus, the B display possessed by ancestral "brevirostris" species probably resembled Bc1 and Bb1 more closely than Bw1, Bw2, or Bw3.

CONCLUSIONS

The data presented here show that each of the three "brevirostris" sibling species possesses a unique display repertoire. Future experimental studies might attempt to determine: (1) whether the displays function in maintaining isolation between adjacent species' gene pools; (2) whether there are functional differences between the Type B displays in *A. websteri* and *A. brevirostris*; and (3) how dewlap color and pulses function as part of the head bob displays. To make the comparative analysis complete, a study describing the display repertoire of *A. marron*, a fourth sibling species which inhabits a small area on the south coast of Haiti, is needed.

Table 1. The number of displays, collecting localities, and display types 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 Forban	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

Table 2. Static display modifiers used by _A_. _websteri_ , _A_. _caudalis_ , and _A_. _brevirostris_, (arranged from most to least frequently observed).

Modifier	Description
Erected Crest	Dorsal fold of skin erected in nuchal area, but when fully expressed crest extends down 2/3 of the body.
Lowered Throat	Hyoid apparatus lowered to give a swollen appearance to the throat region.
Lateral Compression	Rib cage compressed laterally to increase apparent size of trunk when viewed saggitally.
Orbed Eyes	Eyelids widely opened and pupils dialated.
Gaped Mouth	Mouth partially opened.
Protruded Tongue	Tongue projected forward beyond the gaped mouth.

Table 3. Dynamic display modifiers used by *A. websteri*, *A. caudalis* , and *A. brevirostris*.

Modifier	Description
Prior Pulse	The temporally variable dewlap pulse given prior to the stereotyped head bobdisplay (observed in all three species).
Head Roll	The temporally variable raising and lowering of the head before initiation of the stereotyped head bob display. (observed in all three species).
Rapid Head Bobs	Short series of rapidly performed head bobs of shallow amplitude preceding the stereotyped head bob display (observed in all three species).
Tail Lift	The slow arching of the tail at the endof the Type A display (observed only in *A. caudalis*).

Table 4. Kinds and number of 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		
	nondirected	male-male	female-male
_A_. _websteri_	81	39	103
_A_. _caudalis_	39	29	101
_A_. _brevirostris_	3	22	3

	Context: Type B displays		
	nondirected	male-male	female-male
_A_. _websteri_	0	19	31
_A_. _caudalis_	0	43	87
_A_. _brevirostris_	0	14	3

Table 5. The bob number in core the display, the mean core duration the range in core duration, the mean number of dewlap pulses, and the presence or absence of the tail lift modifier in the Type A displays of *A. websteri*, *A. caudalis*, and *A. brevirostris*. Means were obtained from an average for each male and pooled for the species.

Variable	*A. websteri*	*A. caudalis*	*A. brevirostris*
Bob No. in Core Display	5	5	5
Mean (± S.E.) 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 (± S.E.) Number of Dewlap Pulses	1.07 ± .04 (n=17)	2.15 ± .20 (n=18)	.02 ± .02 (n=4)
Tail Lift Modifier	never observed	frequently observed	never observed

Table 6. The mean core duration, the range in core duration, and the coefficient of variation for each mean core duration for 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 (± S.E) for Core Duration	5.54 ± .15	5.58 ± .57	6.41 ± .28
Range in Core Duration	4.9--6.4	5.0--6.2	5.7--6.9
C.V.	9.0	14.5	8.8

Table 7. The variables entered by the stepwise discriminant analysis program for the Type A displays of _A. websteri_, _A. caudalis_ and _A. brevirostris_ 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	Unit3	108.72	.1985	163.00
3	Unit1	111.91	.1069	179.11
4	Pulse No.	39.54	.0820	162.05
5	Unit5	15.60	.0731	139.73
6	Unit9	26.01	.0609	131.29
7	Unit2	11.06	.0560	118.37
8	Unit4	17.57	.0493	112.14
9	Bob No.	10.14	.0456	104.28
10	Unit6	7.70	.0430	97.03
11	Unit7	24.26	.0361	98.03
12	Unit8	12.08	.0330	94.68

Table 8. F-matrix generated from the stepwise discriminant analysis program using the Type A displays of *A. websteri*, *A. caudalis* and *A. brevirostris*. The F-values test the equality of group means for each pair of display groups. d.f.= 12 and 252

	A. brevirostris	*A. caudalis*
A. caudalis	67.25	
A. websteri	59.82	218.12

Table 9. The eigenvalue, percent variance explained and coefficients for each of the two standardized discriminant functions (DF-1, DF-2) produced in the discriminantion of the Type A displays of *A. websteri*, *A. caudalis* and *A. brevirostris*.

	DF-1	DF-2
Eigenvalue	10.42	1.66
Percent of Variance Explained	86.26	13.74
	Coefficients	
Variable		
Unit1	2.65	2.63
Unit2	-1.73	1.81
Unit3	-6.54	-4.92
Unit4	3.48	-3.38
Unit5	5.35	4.88
Unit6	-0.25	5.40
Unit7	5.57	-5.21
Unit8	-2.58	-2.87
Unit9	-7.82	0.93
Pulse No.	.017	-0.70
Bob No.	-.043	-0.19
Tail Lift	-1.83	1.09

Table 10. Jackknifed classification matrix for the discriminant analysis performed on the Type A displays of *A. websteri*, A. caudalis *and* A. brevirostris.

Groups	Percent Correct	*A. websteri*	*A. caudalis*	*A. brevirostris*
A. websteri	98.5	134	0	2
A. caudalis	100.0	0	83	0
A. brevirostris	93.6	2	1	44
Total	93.8			

Table 11. Spearman's rank correlation coefficients and corresponding probabilities for correlations noted between head bob number and each of the first nine unit durations for _A. websteri_ (n=17), _A. caudalis_ (n=17), _A. brevirostris_ (n=8) Type A core display. Results were obtained using only males who varied their total head bob number in their display performances. An * denotes a significant correlation ($p \leq .01$).

Unit Numbers	Correlation Coefficient	Probability
	A. websteri	
1	0.15	0.57
2	0.32	0.21
3	0.45	0.07
4	-0.28	0.28
5	0.63*	0.007
6	0.42	0.09
7	0.72*	0.001
8	0.54	0.02
9	0.74*	0.006
	A. caudalis	
1	0.66*	0.01
2	-0.37	0.16
3	0.31	0.25
4	-0.15	0.58
5	0.67*	0.003
6	0.11	0.68
7	0.62	0.008
8	0.49	0.04
9	0.69*	0.002
	A. brevirostris	
1	0.64	0.09
2	-0.37	0.37
3	0.55	0.16
4	-0.46	0.26
5	0.21	0.62
6	-0.46	0.26
7	0.23	0.58
8	0	1.0
9	0.67	0.07

Table 12. Descriptive statistics for unit durations (in seconds) for the Type A displays of A. websteri (Aw), A. caudalis (Ac), and A. brevirostris (Ab).

	Aw (n=17)				Ac (n=19)			
Unit	Mean	S.E.	95%C.I.	C.V.	Mean	S.E.	95%C.I.	C.V.
1	0.88	.055	.096	25.7	1.01	.036	.063	14.6
2	0.61	.029	.050	19.8	0.60	.022	.038	15.6
3	0.93	.056	.098	25.1	0.46	.017	.030	15.3
4	0.97	.031	.054	13.2	1.15	.030	.052	11.2
5	0.65	.027	.047	17.2	0.54	.021	.036	17.2
6	1.30	.060	.105	18.9	0.89	.036	.062	17.5
7	0.59	.036	.063	25.3	0.34	.021	.036	27.1
8	1.00	.019	.033	8.0	0.68	.033	.057	21.5
9	0.48	.024	.042	21.1	0.21	.016	.028	33.0

	Ab (n=4)			
Unit	Mean	S.E.	95%C.I.	C.V.
1	1.07	.074	.174	13.8
2	0.74	.053	.124	14.3
3	0.64	.079	.186	24.7
4	1.02	.038	.089	7.5
5	0.61	.064	.150	21.0
6	1.24	.074	.174	12.0
7	0.42	.042	.099	20.0
8	0.83	.041	.096	9.9
9	0.33	.025	.059	15.0

Table 13. Qualitative descriptions of the repeating elements in Act2 of each Type B display for _A_. _websteri_ (Bw1, Bw2, Bw3), _A_. _caudalis_ (Bc1), and _A_. _brevirostris_ (Bb1, Bb2).

Variable	Description
Bw1	short-long
Bw2	doubles
Bw3	singles
Bc1	long-short
Bb1	long-short
Bb2	long-short-short

Table 14. The variables entered by the stepwise discriminant analysis program for the Type B displays of *A. websteri* (Bw1-2), *A. caudalis* (Bc1), and *A. brevirostris* (Bb1) 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	Unit12	91.84	.0346	188.25
3	Unit4	94.34	.0108	188.23
4	unit11	45.90	.0052	177.04
5	Unit10	18.50	.0036	155.26
6	Unit3	11.81	.0028	137.60
7	Unit13	7.03	.0024	122.04
8	Unit1	5.69	.0021	109.95

Table 15. F-matrix generated from the stepwise discriminant analysis program using the Type B displays of _A_. _websteri_ (Bw1-2), _A_. _caudalis_ (Bc1), and _A_. _brevirostris_ (Bb1). The F-values test the equality of group means for each pair of groups. d.f.= 8 and 123

	Bw2	Bw1	Bc1
Bw1	144.08		
Bc1	304.93	218.76	
Bb1	63.95	70.55	46.78

Table 16. The eigenvalue, percent variance explained and coefficients for each of the three standardized discriminant functions produced in the discrimination of theType B displays of _A_. _websteri_ (Bw1-2), _A_. _caudalis_ (Bc1), and _A_. _brevirostris_ (Bb1).

	DF-1	DF-2	DF-3
Eigenvalue	23.60	9.15	.91
Percent of Variance Explained	70.1	27.2	2.7
	Coefficients		
Variable			
Unit1	.076	2.75	1.36
Unit3	-1.33	-0.63	6.42
Unit4	2.58	6.18	-1.65
Unit5	6.95	1.88	4.81
Unit10	2.73	0.56	-6.23
Unit11	-5.47	0.23	-2.22
Unit12	-3.23	-9.76	-2.57
Unit13	6.20	-7.12	2.65

Table 17. Jackknifed classification matrix for the discriminant analysis performed on the Type B displays of _A_. _websteri_ (Bw1-2), _A_. _caudalis_ (Bc1), and _A_. _brevirostris_ (Bb1).

Groups	Percent Correct	Bw1	Bw2	Bc1	Bb1
Bw1	100.00	13	0	0	0
Bw2	100.00	0	18	0	0
Bc1	100.00	0	0	92	0
Bb1	90.0	0	0	1	10
Total	99.3				

Table 18. Descriptive satistics for unit durations (in seconds) for the Type B displays of *A. websteri* (Bw1-3), *A. caudalis* (Bc1), and *A. brevirostris* (Bb1-2).

	Bw1 (N=9)				Bw2 (N=13)			
Unit	Mean	S.E.	95%C.I.	C.V.	Mean	S.E.	95%C.I.	C.V.
1	0.36	.030	.058	22.5	0.68	.048	.087	24.5
2	0.61	.057	.113	25.1	0.04	.016	.029	130.1
3	0.45	.021	.040	13.2	0.28	.027	.048	33.2
4	0.29	.019	.036	18.4	0.73	.029	.052	14.5
5	0.89	.030	.057	9.6	0.89	.029	.052	11.8
6	1.28	.050	.095	11.1	1.19	.050	.089	15.0
7	0.40	.036	.067	26.4	0.48	.016	.029	12.0
8	0.92	.057	.106	8.6	0.09	.018	.032	72.3
9	0.70	.024	.045	10.2	0.52	.028	.050	19.4
10	0.77	.018	.033	7.1	0.71	.025	.044	12.7
11	0.26	.019	.035	22.3	0.31	.011	.020	13.5
12	0.91	.126	.234	41.4	0.06	.013	.024	75.8
13	0.61	.025	.047	12.1	0.40	.018	.033	16.5

	Bw3 (N=6)				Bc1 (N=24)			
Unit	Mean	S.E.	95%C.I.	C.V.	Mean	S.E.	95%C.I.	C.V.
1	0.53	.075	.176	31.7	0.21	.020	.034	45.3
2	0.03	.013	.027	129.2	0.21	.020	.034	45.3
3	0.21	.020	.044	52.2	0.80	.034	.058	11.4
4	1.45	.176	.375	21.8	0.56	.019	.033	21.1
5	0.74	.090	.192	27.2	0.28	.013	.023	22.9
6	1.45	.099	.212	15.4	1.15	.054	.093	22.5
7	0.68	.036	.077	11.8	1.23	.033	.056	13.1
8	1.16	.074	.149	15.6	0.40	.032	.054	38.7
9	0.64	.077	.154	29.2	0.21	.008	.013	17.8
10	0.89	.045	.091	12.5	0.43	.014	.024	16.1
11	0.53	.055	.110	25.4	0.99	.022	.039	11.1
12	0.77	.048	.097	15.4	0.30	.024	.041	37.9
13	0.47	.044	.090	23.1	0.17	.007	.011	18.4
14	0.65	.053	.108	20.1				
15	0.40	.035	.071	21.4				

Table 18. (continued).

	Bb1 (N=4)				Bb2 (N=4)			
Unit	Mean	S.E.	95%C.I.	C.V.	Mean	S.E.	95%C.I.	C.V.
1	0.41	.073	.171	35.7	0.41	.057	.134	28.2
2	0.27	.070	.165	52.3	0.67	.055	.129	16.3
3	0.40	.050	.118	25.0	0.35	.023	.054	13.3
4	0.73	.039	.092	10.8	0.48	.035	.082	14.4
5	0.50	.028	.066	11.4	0.36	.015	.035	8.4
6	1.46	.059	.139	8.1	1.59	.030	.071	3.8
7	0.77	.044	.104	11.4	0.72	.046	.108	12.8
8	0.55	.040	.094	14.5	0.68	.030	.071	8.7
9	0.32	.011	.026	6.9	0.28	.017	.040	12.0
10	0.81	.040	.094	9.9	0.36	.019	.045	10.7
11	0.65	.045	.106	13.7	0.29	.019	.045	13.4
12	0.43	.030	.071	14.2	1.00	.022	.052	4.5
13	0.26	.014	.033	11.1	0.67	.027	.064	8.0
14					0.63	.017	.040	5.2
15					0.28	.006	.014	4.4
16					0.32	.022	.052	13.5
17					0.25	.010	.024	8.0

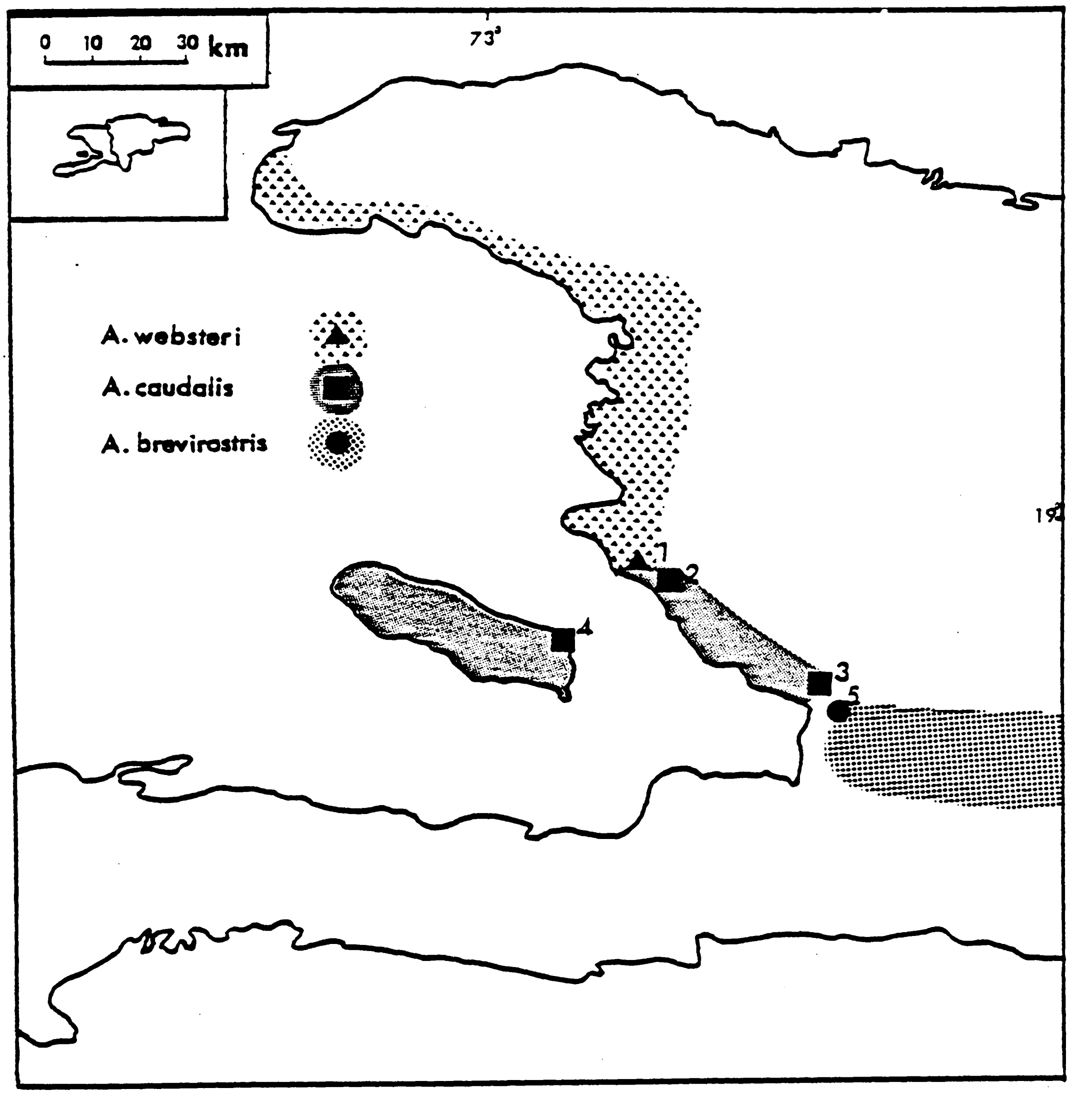

Fig. 1. Probable species distributions and collecting sites for *A. websteri* (1, Montrouis), *A. caudalis* (2, Trou Forban; 3, Source Matelas; 4, Ile de la Gonave), and *A. brevirostris* (5, Daspinasse).

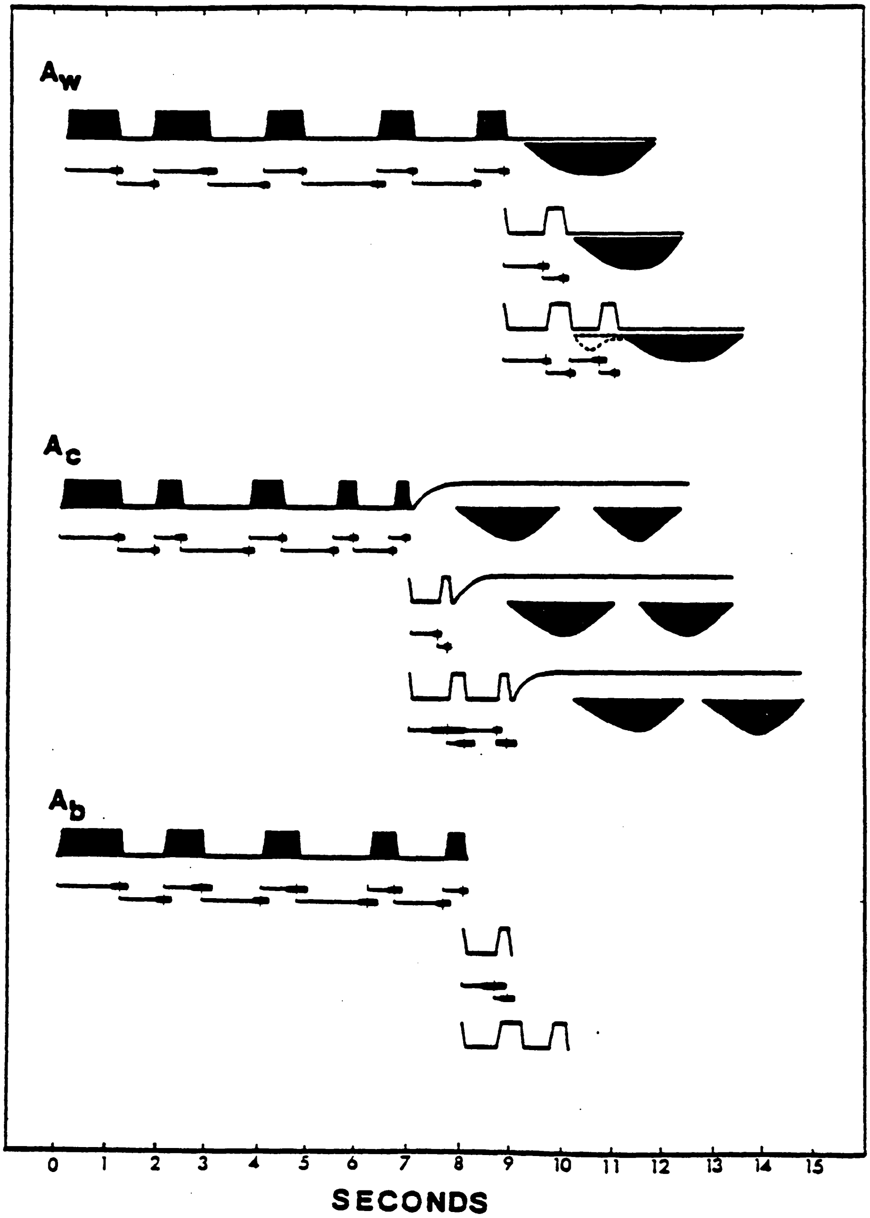

Fig. 2. Average Type A display of A.websteri (Aw), A. caudalis(Ac), and A. brevirostris (Ab), showing the five bob core display (blocked in head bobs) and optional additional bobs (outlined bobs). Horizontal lines below bobs and interbob pauses show the display units vertical lines give the unit mean durations, and the horizontal black bars show the 95 % confidence intervals of unit means.

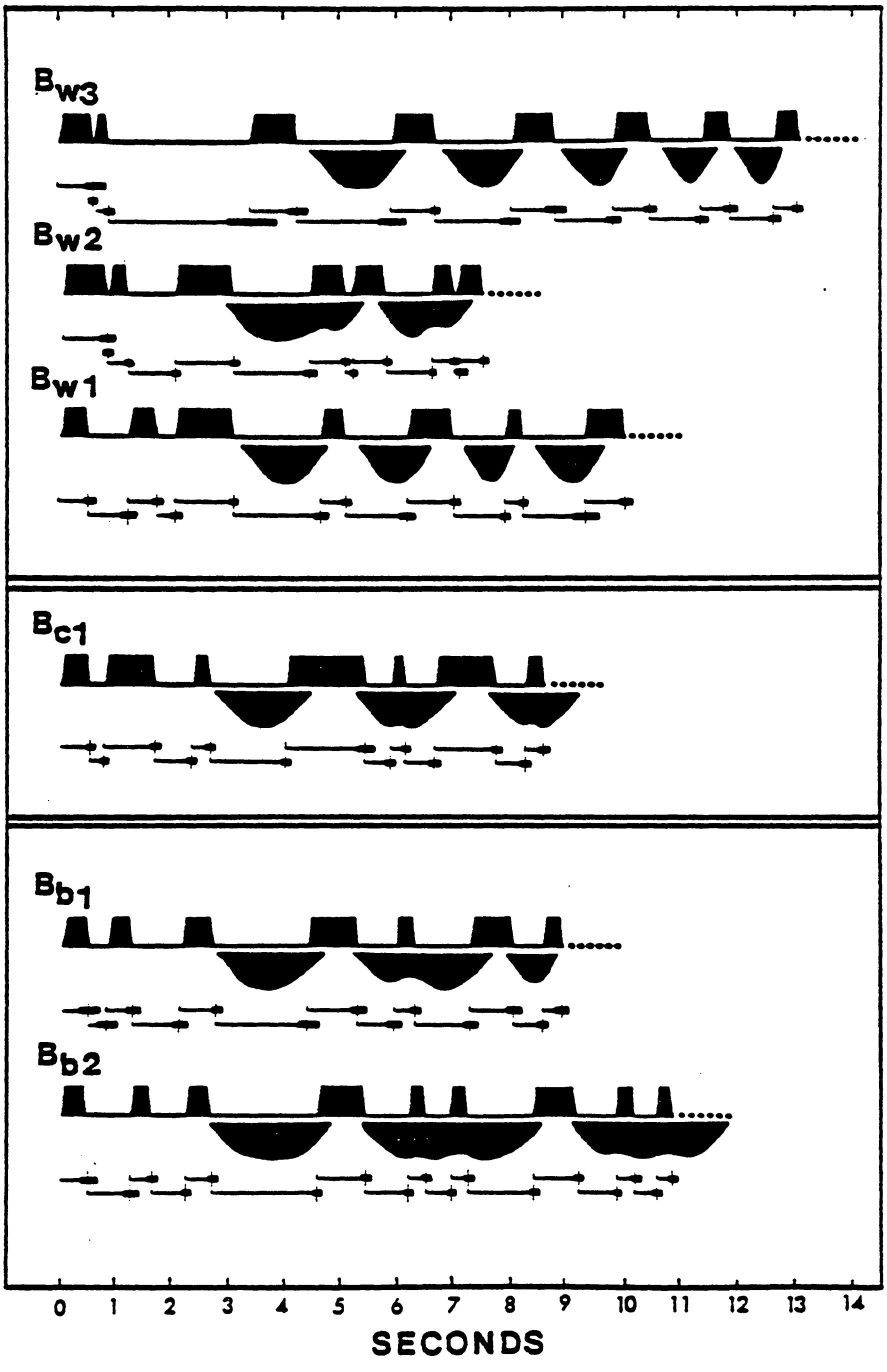

Fig. 3. Average Type B DAP graphs for A. websteri (Bw1-3), A. caudalis (Bc1) and A. brevirostris (Bb1-2,). See Fig. 2 for notation for descriptive statistics of unit durations.

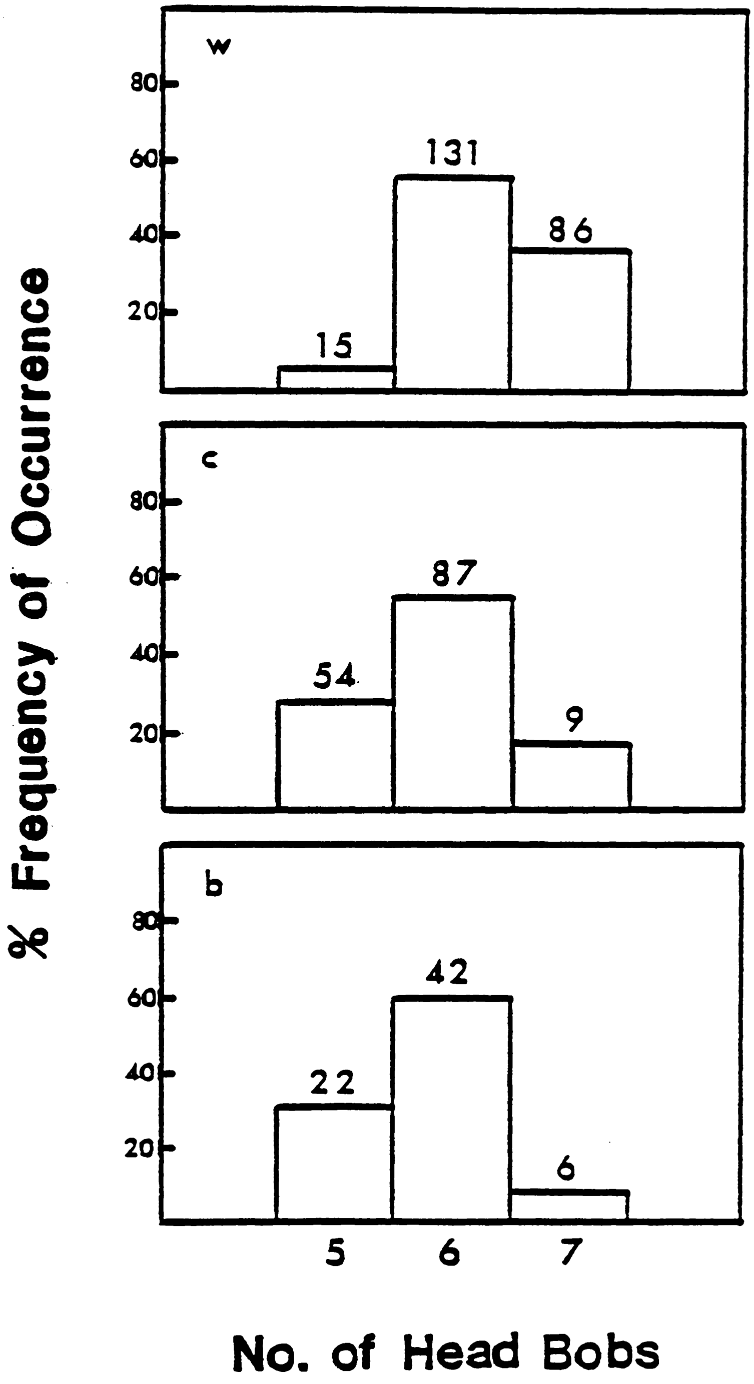

Fig. 4. The number of bobs performed in the Type A displays of A. websteri (w), A. caudalis (c), and A. brevirostris (b). Numbers over bars are sample sizes.

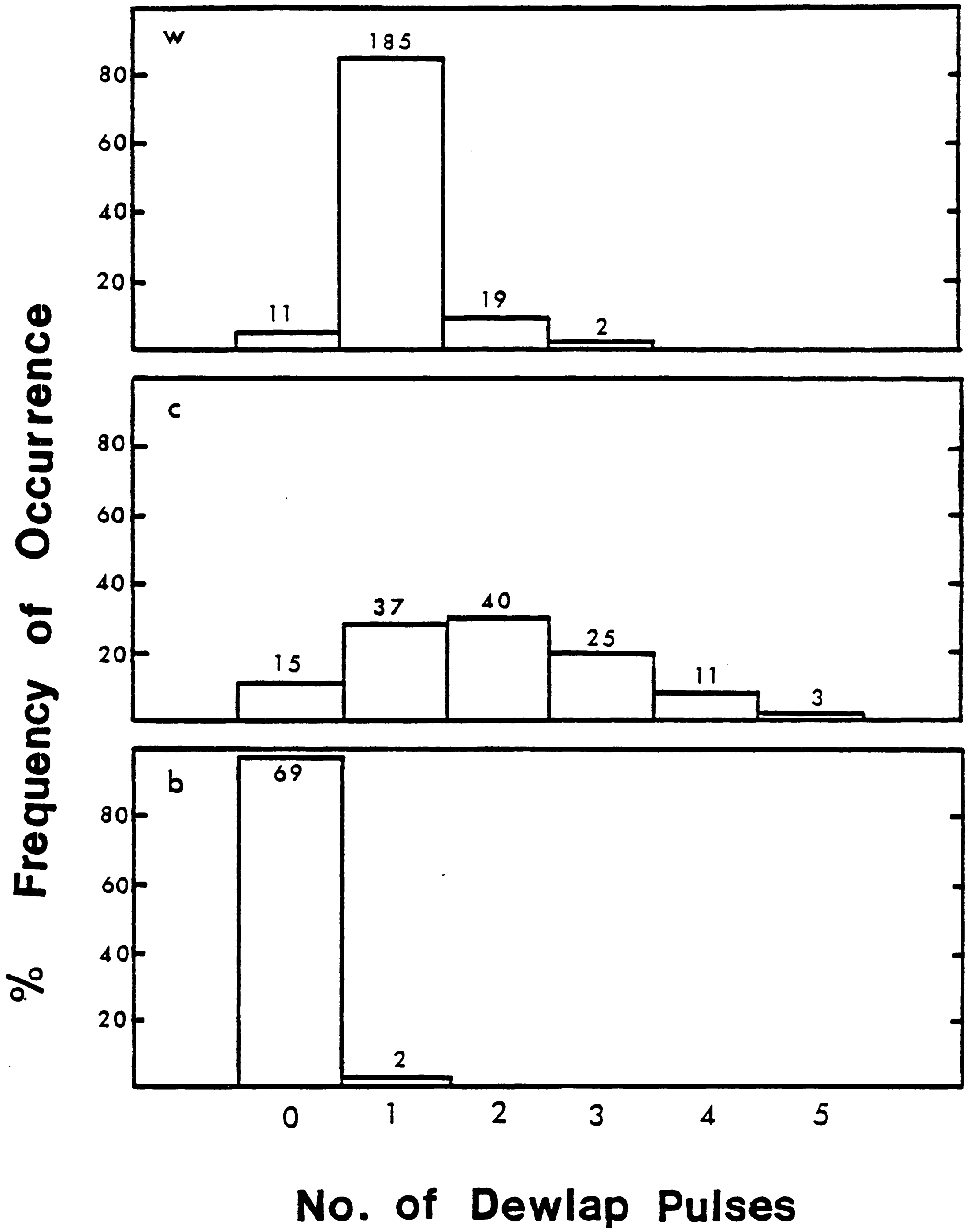

Fig. 5. The number of dewlap pulses performed at the end of the Type A displays of A. webster (w) A. caudalis (c), and A. brevirostris (b). Numbers over bars are sample sizes.

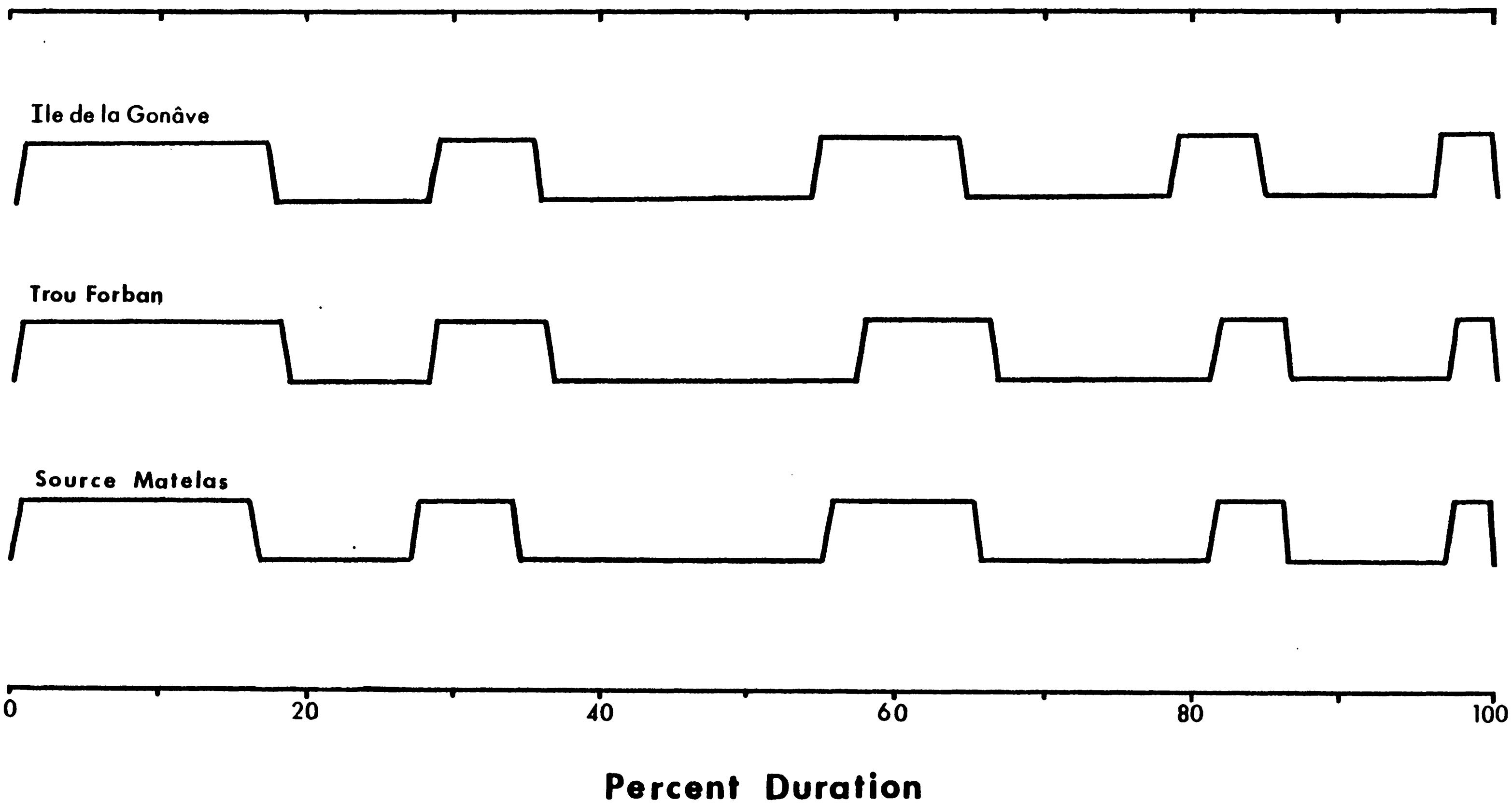

Fig. 6. Average Type A DAPs for A. caudalis males from: Ile de la Gonave (n=5), Trou Forban (n=12), and Source Matelas (n=2). Units are expressed as a percentage of the core duration (total of first nine units). Values are means obtained from an average for each male, pooled for each collecting localitiy.

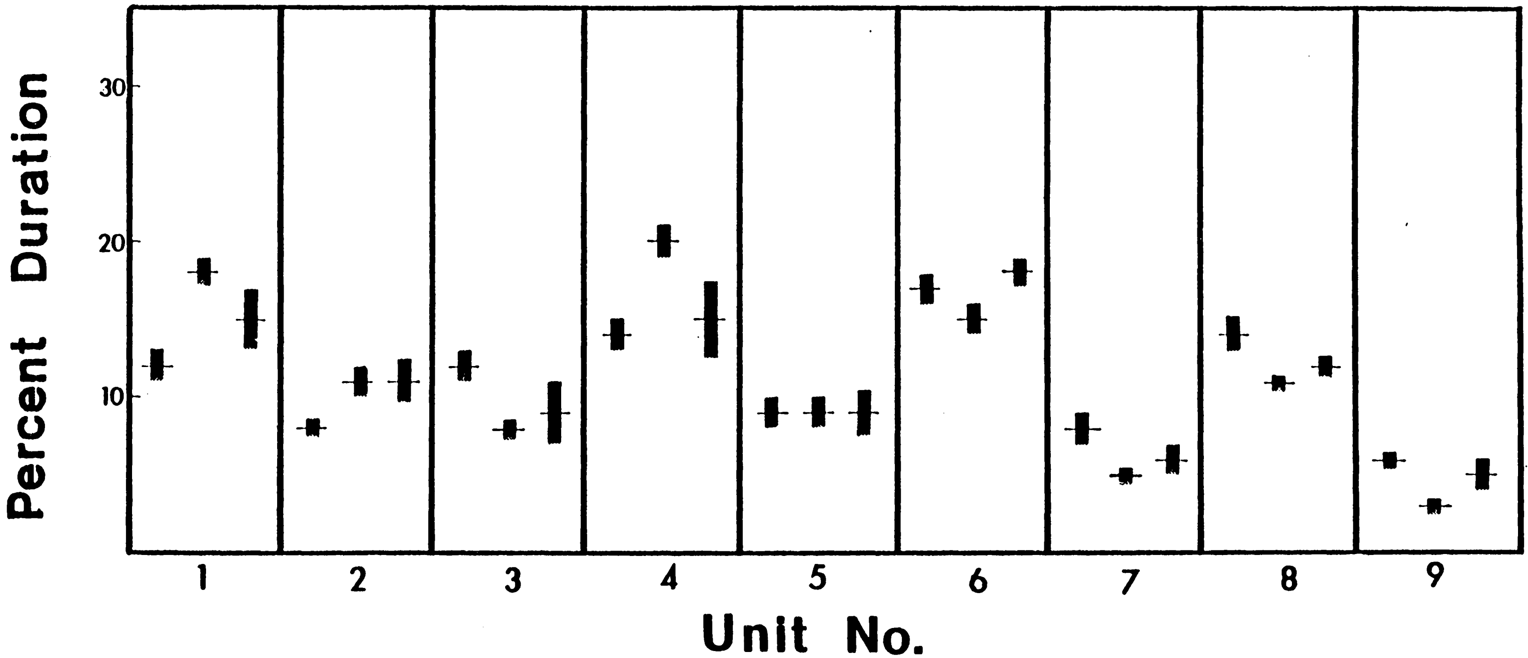

Fig. 7. Unit durations of the Type A core displays. Horizontal lines are unit means and bars are 95 % confidence intervals for unit durations. For a given unit, the species are arranged from left to right: A. websteri, A. caudalis, and A. brevirostris.

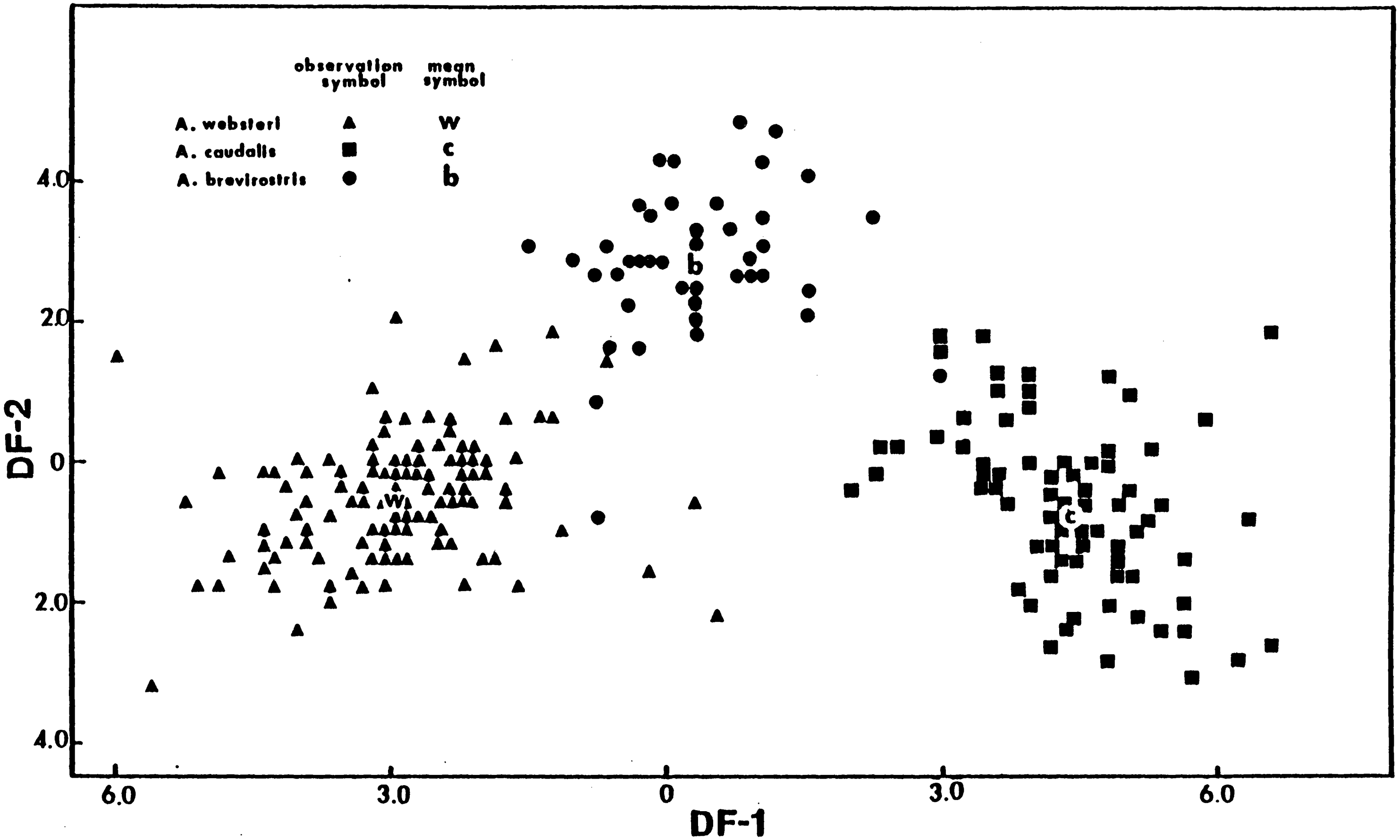

Fig. 8. Display observations and group means of the discriminant analysis for the Type A displays of A. websteri, A. caudalis, and A. brevirostris using the standardized discriminant funcions (DF-1 and DF-2) as the axes.

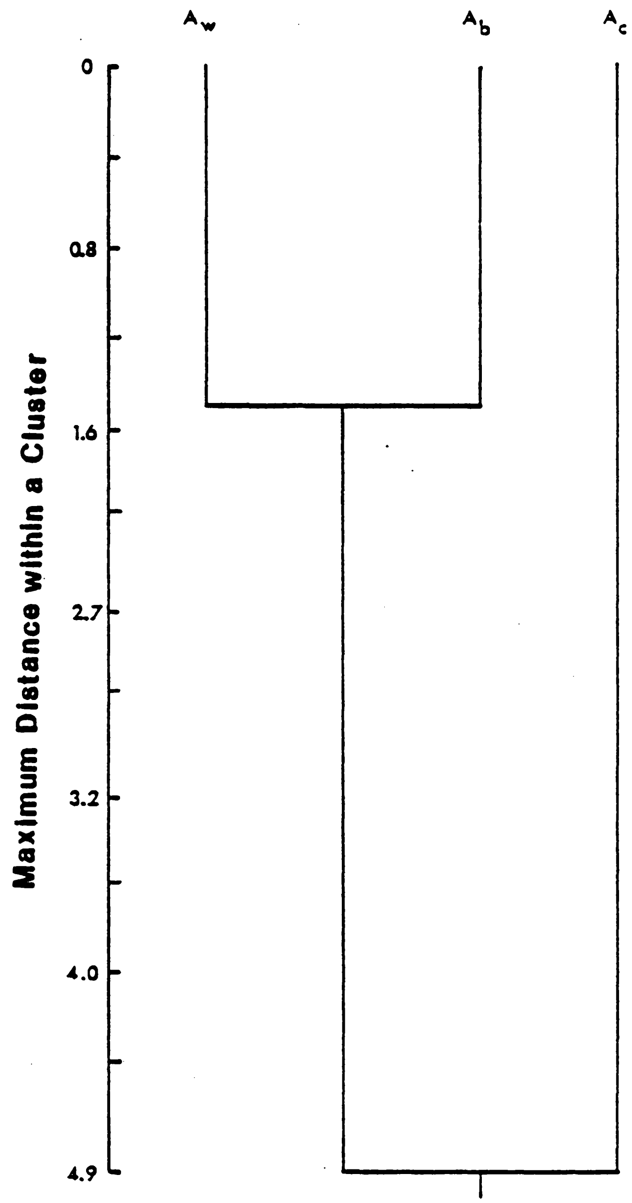

Fig. 9. Phenogram for the Type A displays of A. websteri, A. caudalis, and A. brevirostris.

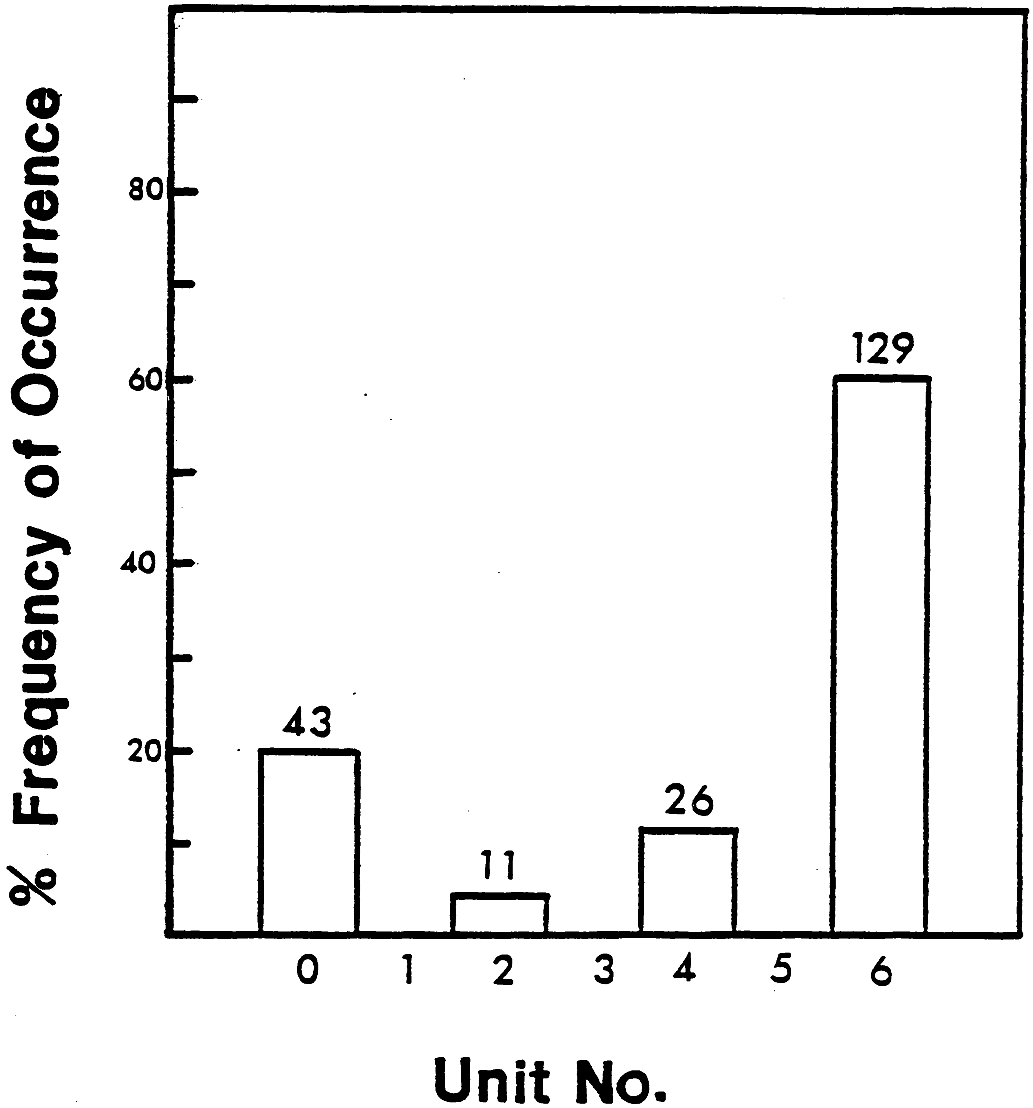

Fig. 10. The unit during which the dewlap was first pulsed in the the Type B displays (0=before first head bob, odd units depict bobs, even units depict interbob pauses). Numbers over bars are sample sizes.

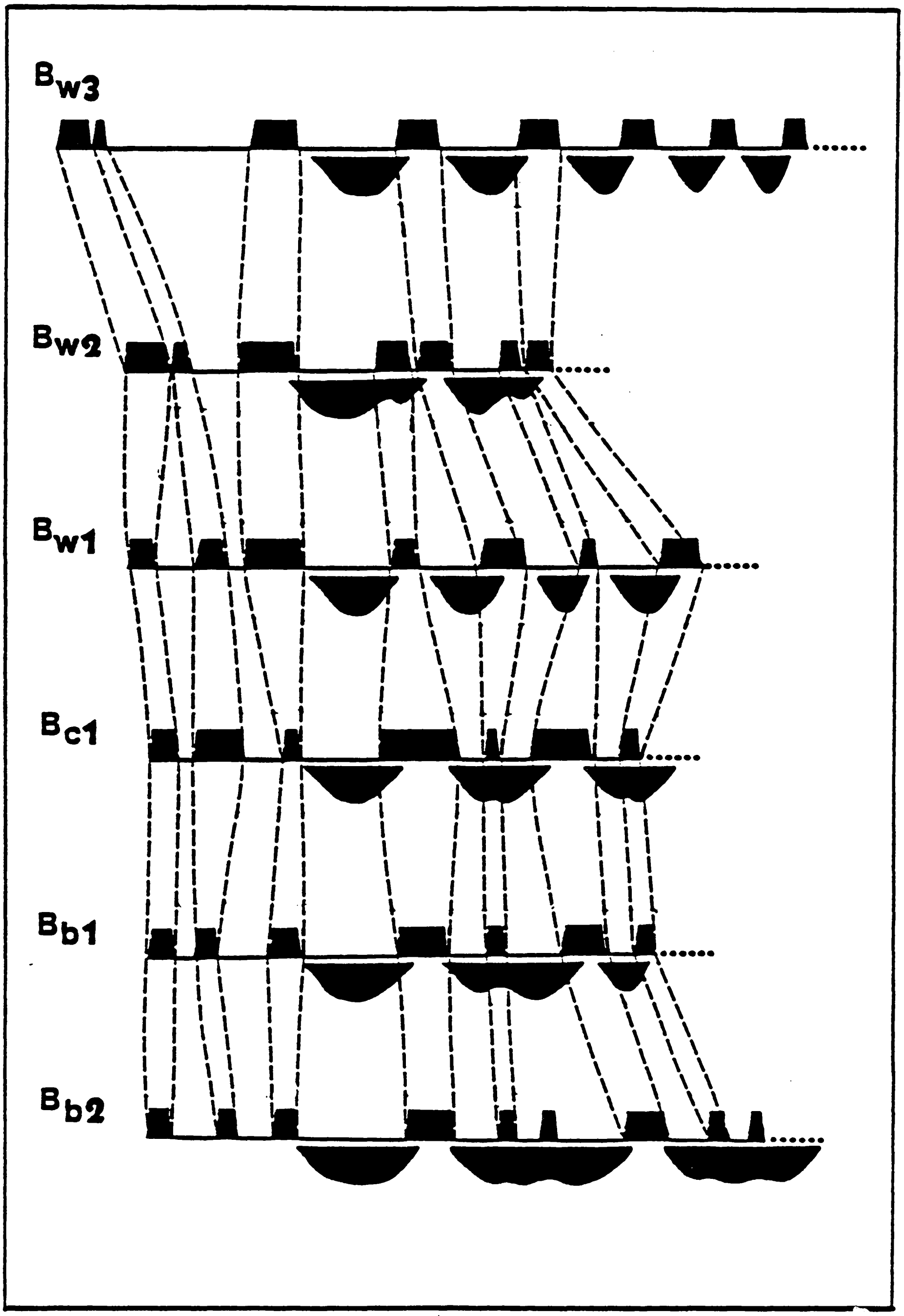

Fig. 11. Postulated homologous head bobs (enclosed in dashed lines) for the Type B displays of A. websteri (Bw1-3), A. caudalis (Bc1), and A. brevirostris$ (Bb1-2).

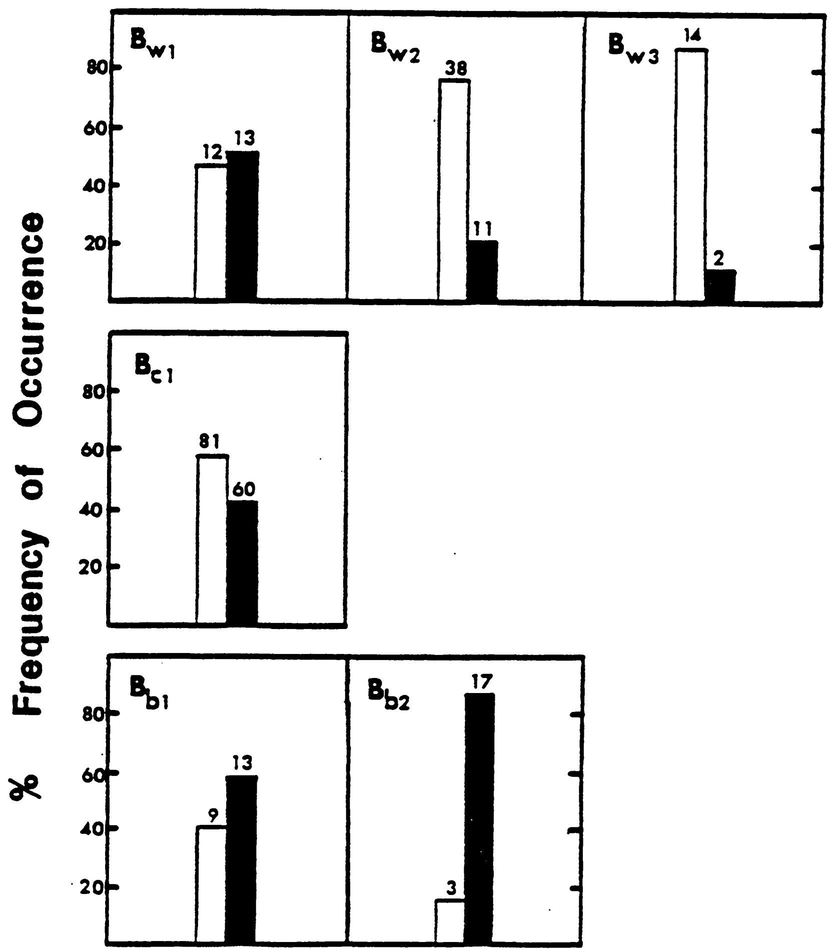

Fig. 12. The number of static modifiers accompanying the Type B Displays of A. websteri (Bw1-3), A. caudalis, (Bc1) and A. brevirostris (Bb1-2). Open bars represent 0-2 modifiers and black bars represent 3-5 modifiers. Numbers over bars are sample sizes.

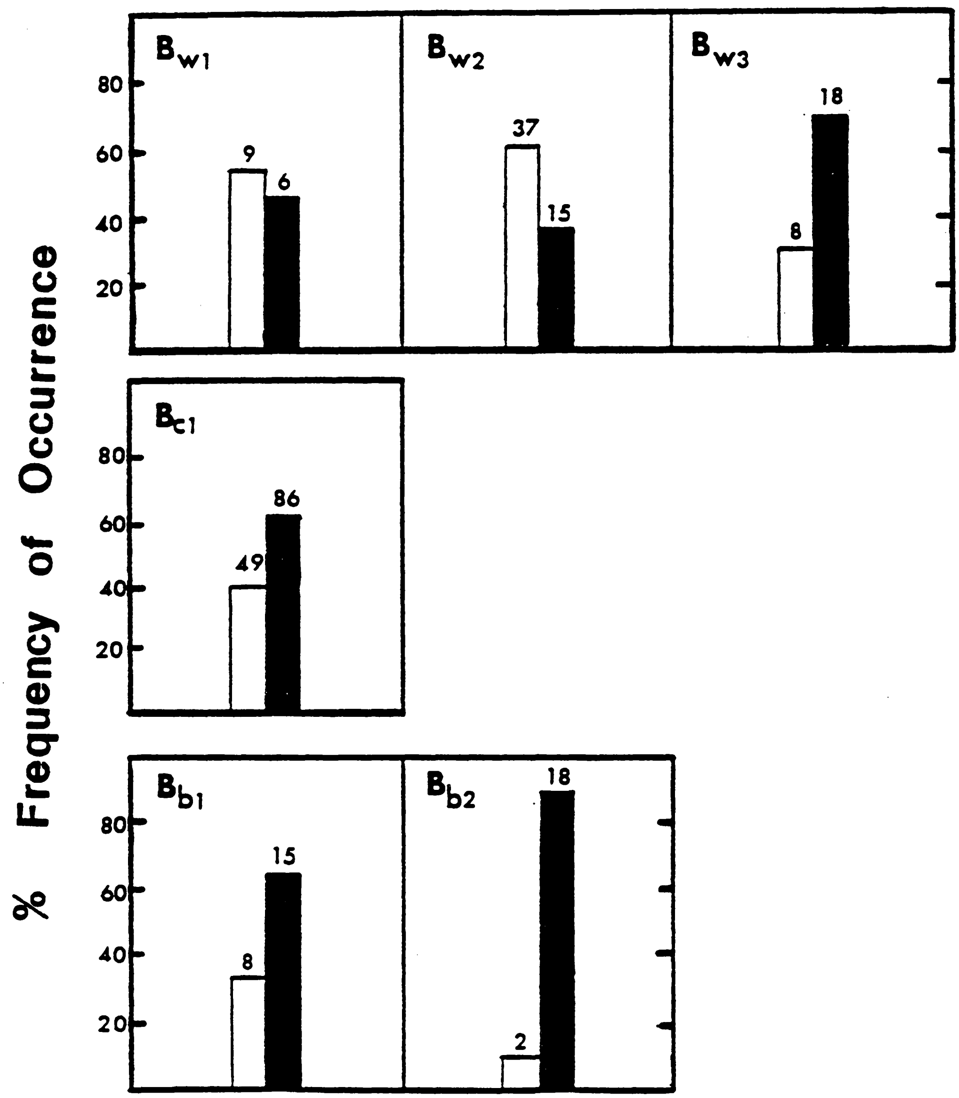

Fig. 13. Use of forelimbs only (open bars), or all four limbs (solid bars) during Type B Displays of A. websteri (Bw1-3) A. caudalis (Bc1), and A. brevirostris(Bb1-2). Numbers over bars give sample sizes.

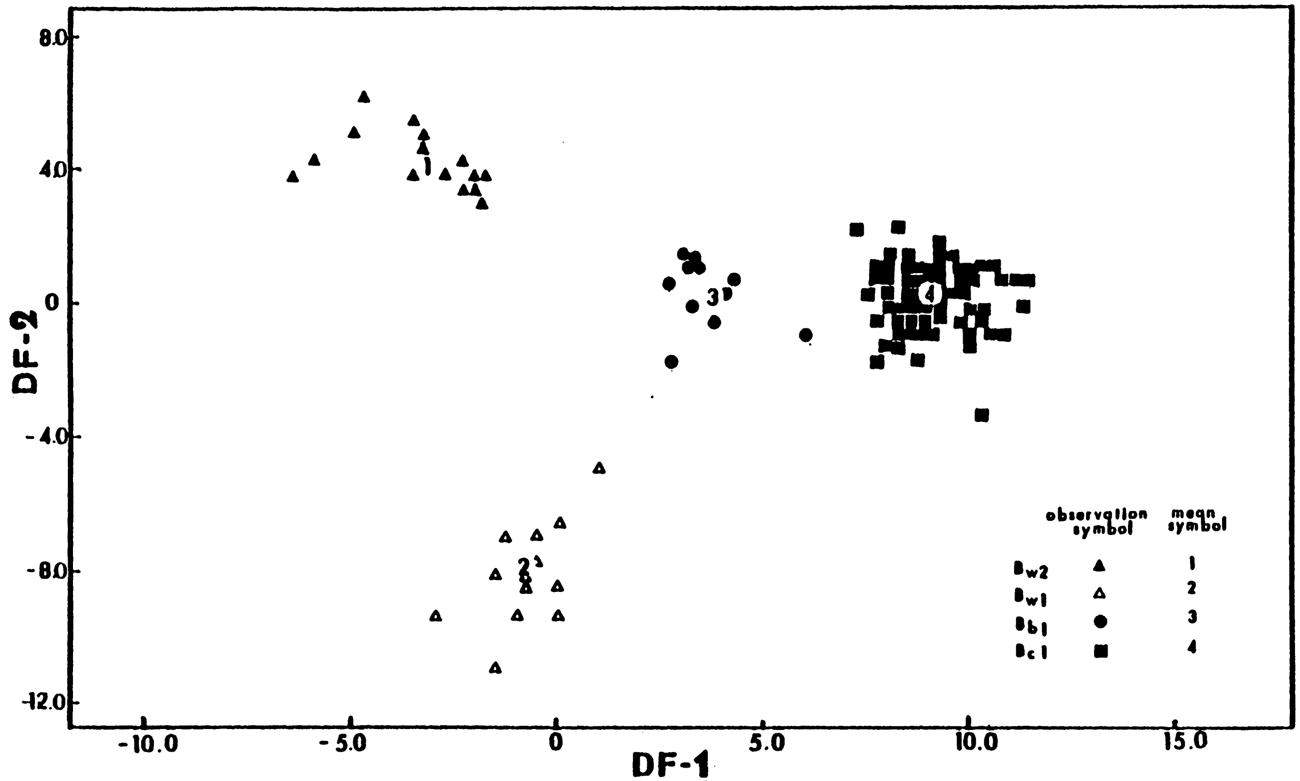

Fig. 14. Display observations and group means of the discriminant analysis for the Type B displays of A. websteri (Bw1-2), A. caudalis (Bc1), and A. brevirostris (Bb1) using thestandardized discriminant functions (DF-1 and DF-2) as the axes.

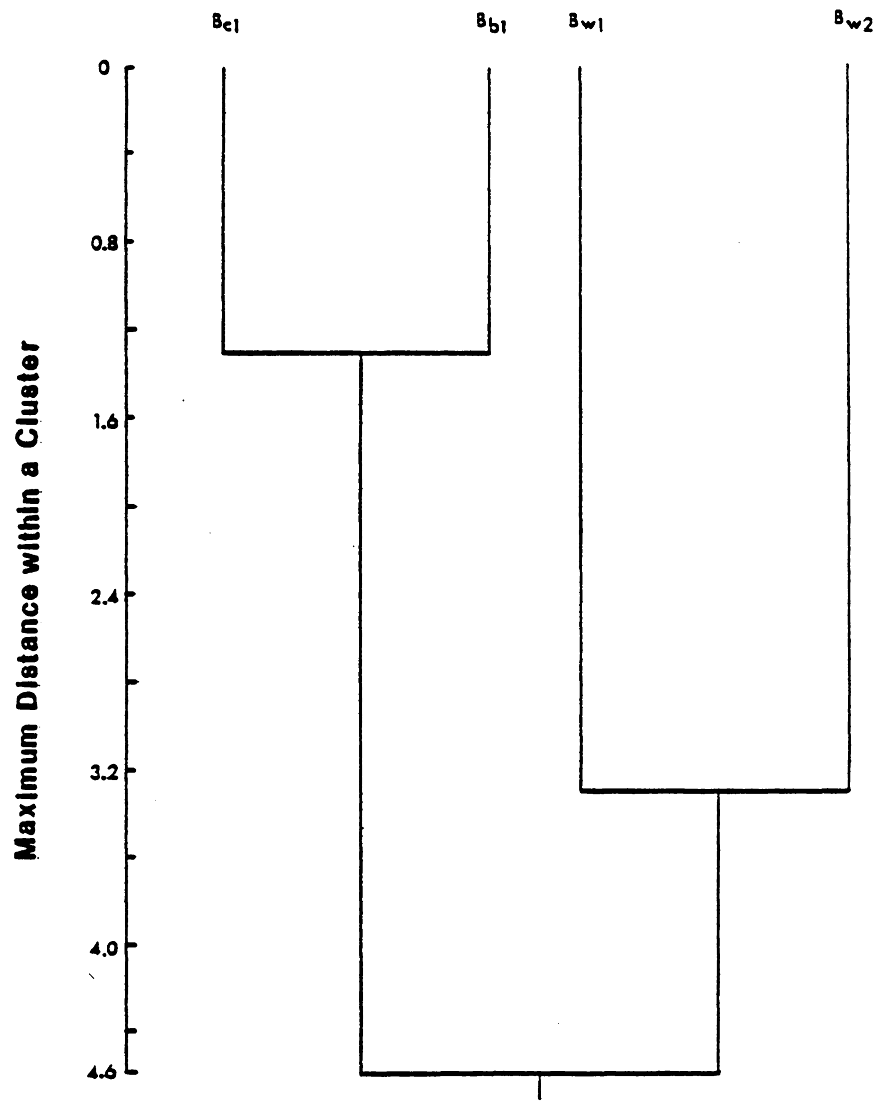

Fig. 15. Phenogram of the Type B displays of A. *websteri* (Bw1-3), A. *caudalis* (Bc1), and A. *brevirostris* (Bb1-2).

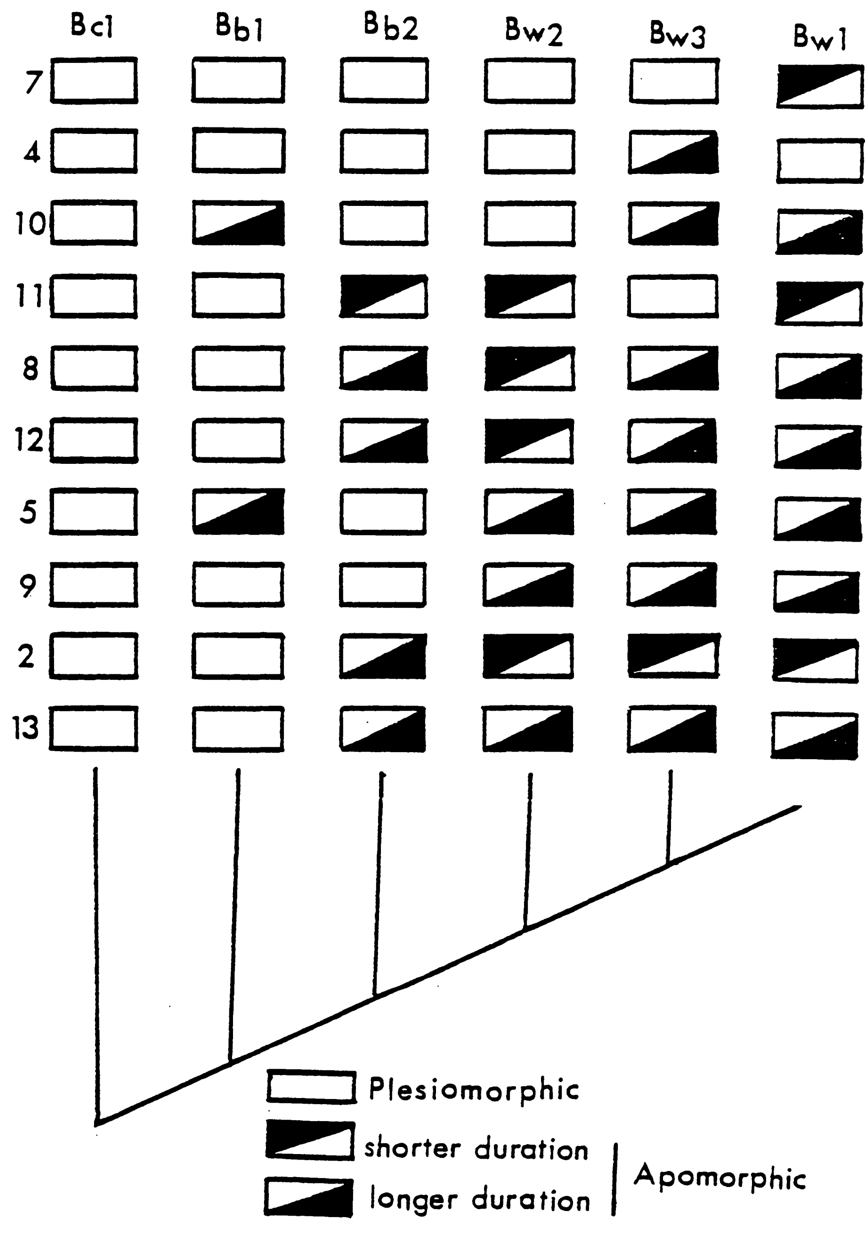

Fig. 16. Cladogram of the Type B displays of _A. websteri_ (Bw1-3), _A. caudalis_ (Bc1), and _A. brevirostris_ (Bb1-2).

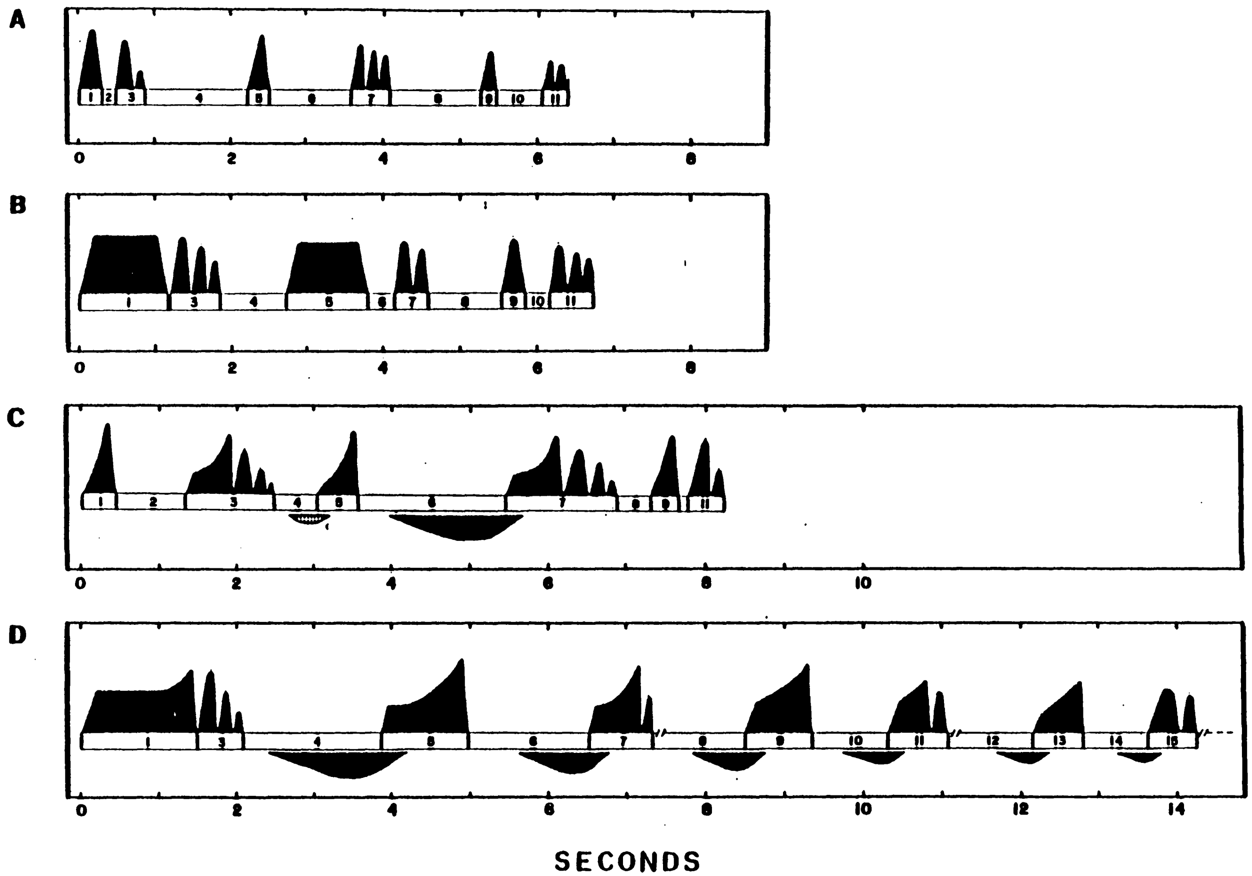

Fig. 17. Four of the six display types of <u>Anolis distichus</u> (Jenssen, 1982).

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 Institute Inc., Raleigh, N.C.

Barlow, G. W. 1977. Modal Action Patterns. In: How Animals Communicate. T. A. Sebeok (ed.). Indiana University Press, Bloomington & London. pp. 100-105.

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.

Etheridge, R. 1960. The relationships of the anoles (Reptilia: Sauria: Iguanidae): An interpretation based on skeletal morphology. PhD. thesis. Univ. Michigan, Ann Arbor. p. 236.

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

Jenrich, R. and P. Sampson. 1979. Stepwise Discriminant Analsysis. In: Biomedical Computer Programs P-Series. W. J. Dixon and M. B. Brown (eds.). University of California Press, Berkeley. pp. 711-747

Jenssen, T. A. 1971. Display analysis of Anolis nebulosus (Sauria: Iguanidae). Copeia 1971:197-209.

Jenssen, T. A. 1977. Evolution of anoline lizard display behavior. Am. Zool. 17:203-216.

Jenssen, T. A. 1978. Display diversity in anoline lizards and problems of interpretation. In: Behavior and neurology of lizards: An interdisciplinary conference. N. Greenberg and P. D. MacLean (eds.). N.I.M.H., Rockville, Maryland. pp. 269-285.

Jenssen, T. A. 1979. Display modifiers of Anolis opalinus (Lacertilia: Iguanidae). Herpetologica 35:21-30.

Jenssen, T. A. 1982. Display behavior of two Haitian lizards Anolis cybotes and Anolis distichus. In: Advances in Herpetology and Evolutionary Biology. A. Rhodin, S. Rhodin, and K. Miyata (eds). Harvard Univ. Press, Cambridge, Massachusetts.

Jenssen, T. A. and L. Rothblum. 1977. Display repertoire analysis of Anolis townsendi (Sauria: Iguanidae). from Cocos Island. Copeia 1977:103-109.

Klecka, W. R. 1975. Discriminant Analysis. In: SPSS: Statistical Package for the Social Sciences, 2nd ed. N. H. Nie, C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent (eds.). McGraw-Hill Book Company, New York. pp. 434-467.

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. 1977. Hybridization of Hispaniolan lizards in the Anolis distichus species group. In: The Third Anolis Newsletter. E. E. Williams (ed.). Mus. Comp. Zool., Harvard Univ., Cambridge, Massachusetts. pp.166-170.

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 D. Crews. 1977. Hormones, reproductive behavior, and speciation. Amer. Zool. 17:271-286.

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

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