

Display Behavior of *Anolis bahorucoensis*: an Anole with a Diminutive Dewlap

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ABSTRACT.—Both sexes of *Anolis bahorucoensis* possess a diminutive dewlap, a rare condition reported for only 14 of the 300+ species of anoles. The characteristically large and colorful dewlap of anoline lizards is intimately tied to species-specific stereotypic headbob displays. Both the dewlap and headbob displays have important roles in communication and social structure. Because diminutive size infers loss or reduction of dewlap function, we suspected that the display behavior of *A. bahorucoensis* might also be atypical. We found a signal repertoire typical of the genus, with three species-specific and stereotypic display patterns and several common display modifiers. However, a unique signal design, atypical dewlap use, infrequent display rates, and nonritualized male aggression were unusual departures from the norm. We suggest that the typical and atypical display traits of *A. bahorucoensis* infer significant counterselection pressures that have retained display functions, yet resulted in highly modified display traits. Though field data are required for confirmation, we suggest that intense predation pressure from visually-cued syntopic anoles has been a primary selective agent for the evolution of the atypical display traits and diminutive dewlap size of *A. bahorucoensis*.

INTRODUCTION

A hallmark feature of anoline lizards is the dewlap, a large and colorful flap of throat skin extended by a modified hyoid apparatus (Font and Rome, 1990). The dewlap is a dedicated structure for visual signalling (Jenssen, 1977). Dewlap extension accompanies the species-specific, stereotypic headbob displays of anoles, and serves to increase a display's conspicuousness (Fleishman, 1988a, 1988b, 1992). These visual displays are fundamental to anoline social behavior, and may serve as signals for recognizing conspecifics (e.g. Jenssen, 1971; Losos, 1985a; Macedonia and Stamps, 1994), advertising the boundaries of territories (e.g. Greenberg and Noble, 1944), intimidating opponents (e.g. Greenberg and Noble, 1944; Cooper, 1977; DeCourcy and Jenssen 1994), and advertising sexual receptivity (e.g. Evans, 1938; Greenberg and Noble, 1944; Cooper, 1979).

A diminutive dewlap is a dramatic departure from the enlarged hyoid apparatus typical of anoles and would suggest an atypical signal design and perhaps signal function as well. Such a dewlap is indeed rare in this genus of 300+ species, having

been documented in only 14 species (*Anolis agassizi*, *A. poncensis*, *A. trinitatis*, *A. aliniger*, *A. bahorucoensis*, *A. dolichocephalus*, *A. hendersoni*, *A. monticola*, *A. rupinae*, *A. singularis*, *A. bartschi*, *A. juangundlachi*, *A. ophiolepis*, and *A. vermiculatus*; Schwartz and Henderson, 1991). No obvious factor is shared among the 14 species to suggest a single explanation for this curious anomaly. Although some of these species are probably descendants of common ancestors (e.g., *A. bahorucoensis*, *A. dolichocephalus*, and *A. hendersoni*; Schwartz, 1978), most are not restricted to one phylogenetic subset of *Anolis* and are represented in half of the 14 species series based on osteological characters (Williams, 1976) and in six of the 20 species series based on molecular data (Burnell and Hedges, 1990). The species with diminutive dewlaps are not limited to a particular habitat type and may be found in shady mesophilic forest, xeric open areas, on cliff faces, and even in an aquatic association (Schwartz and Henderson, 1991). In addition, most of the species with diminutive dewlaps are syntopic with congeners having typically-sized dewlaps.

The diminutive dewlap condition may represent one of the following evolutionary

paths: (1) an ancestral state which existed before the selection for enhanced visual displays; (2) the relaxation of selection pressures which were maintaining an enlarged signalling structure; or (3) a prevalent counterselection pressure. The first condition is least likely because the small dewlap state has evolved independently in several species groups and within species groups of recent origins (e.g., *A. ophiolepis*; Burnell and Hedges, 1990; Hass et al., 1993). The latter possibilities are more probable and suggest a reduction in dewlap size because the functional benefits of a large dewlap had decreased or because conventional displays became too costly. Too little is known about the display traits, social behavior, and ecology of the 14 species with reduced dewlaps to suggest alternative conditions under which dewlap reduction may have been selected.

Within a laboratory setting, we examined the display structure and behavior of *Anolis bahorucoensis* (ssp. *bahorucoensis*), a slender anole endemic to the Sierra de Baoruco, Hispaniola (Schwartz and Henderson, 1991). The species is sexually dimorphic, with males being about 20% larger and more brilliantly colored than females. Both sexes possess a very small dewlap (12 mm²; Fig. 1; Orrell, 1994). If a diminutive dewlap is the result of unusual selection pressures, we expected to find a series of related traits which would be concordant with a common shift in signal structure and function. Thus, our objectives were to: (1) document the species' social behaviors and headbob displays; (2) identify the potential functional role of signalling behaviors by quantifying their use under controlled social contexts (e.g., male-alone, male-male and male-female); (3) evaluate whether signal design and use by *A. bahorucoensis* deviates from that typical of other anoles; (4) evaluate *A. bahorucoensis* display behavior for characteristics which might be related to the diminutive-dewlap state; and (5) evaluate potential hypotheses for the evolution of diminutive dewlap size in *A. bahorucoensis*.

MATERIALS AND METHODS

The seven males (\bar{x} snout-vent-length [SVL] = 45.8 ± 0.74 [SE] mm, \bar{x} mass = 2.5 ±

0.08 g) and three females (\bar{x} SVL = 37.3 ± 0.27 mm, \bar{x} mass = 1.3 ± 0.08 g) used in this study were collected from the Sierra de Baoruco by J. Losos. Lizards were housed individually or in male/female pairs in wooden holding cages (0.6 × 0.6 × 0.7 m or 1.2 × 0.6 × 0.8 m). A large observation cage (2.4 × 0.6 × 0.8 m) was divided by a removable opaque partition into two compartments of equal size. The glass front wall was slanted and covered on the inside surface with nylon window screen to reduce the chance of lizards responding to their own reflections. Cages were furnished with tree trunks, branches, artificial foliage, and soil substrate. Cage temperatures ranged from 23°C during the day to 20°C at night. Cage lights were maintained on a 12/12 L:D regime to approximate a natural photoperiod. Because a light intensity of over 200 lux caused lizards to hide, we used a fluorescent black lamp (UV source) and cool white lamp (40 W) over each cage. This combination of lamps provided a light intensity of about 68 lux, which is closer to the 15 lux estimated for the species' forest habitat (Orrell, 1994). Vitamin-dusted crickets, waxworm larvae, and sprayed water were provided daily.

We videotaped observations using a two camera system to simultaneously record display exchanges between two lizards (DeCourcy and Jenssen, 1994; Orrell, 1994). Because signal use as individuals approach one another may suggest additional information about function and the potential arousal of subjects (e.g., DeCourcy and Jenssen, 1994), the separation distance between the two lizards was dictated onto the videotape audio track. Three categories of separation distance were used (greater than 80 cm, 40-80 cm, and less than 40 cm). Because the lizards were very wary of disturbance, observations were made from a darkened blind 1.5 m from the experimental cages.

Display behavior was stimulated using two protocols to create four social contexts. In the first protocol, a male was placed on each side of the observation cage with the central partition in place. This created the male-alone (M-A) context for the purpose of identifying potential territorial adver-

tisement behaviors. Following a three-day acclimation period, the M-A behaviors of each lizard were videotaped for 20 min. Then, the partition was removed to produce the male-male (M-M) context, used to identify agonistic signals. Immediately after the partition was removed, the behaviors of both males were recorded for 60 min. Twenty-four M-A and 12 M-M trials were conducted, pairing nonfamiliar males for each M-M encounter. Since only seven males were available, each male was used three or four times and was given a minimum rest interval of 10 days between trials.

In the second protocol, a male and a female pair were placed in the $1.2 \times 0.6 \times 0.8$ m observation cage at least one week prior to observations. This created the male-resident female context (M-RF) used to identify potential courtship signals. Following the acclimation period, behaviors of the M-RF context were videotaped for a minimum of 30 min. Because pilot studies of the M-RF context revealed a very low activity level, a second type of male-female interaction based on the Coolidge effect (Dewsbury, 1981) was designed to intensify male courtship and display behavior. Male-resident female/strange female context (M-RF/SF) was created by introducing a strange female into the resident pair's cage via a covert release box. The ensuing behavior was videotaped for 30-80 min. The trial was terminated when the strange female hid for at least 10 min. Four male and three female subjects were used to videotape 12 M-RF and 12 M-RF/SF trials, rotating individuals as strange females.

Videotapes were analyzed frame-by-frame to determine the kinds, occurrences, and durations of signalling behaviors. The kinds of displays and their stereotypy were determined by the Display-Action-Pattern (DAP) graph method (see DeCoursey and Jenssen, 1994), which entails plotting the vertical amplitude of the lizard's head (y-axis) over elapsed time (x-axis) for each display. DAP-graphed displays were then divided into the naturally occurring sequential 'units' (Drummond, 1982) that defined the cadence pattern of a display. Displays sharing a common cadence were

categorized as being of the same display 'type.'

For each DAP-graphed display, we recorded: (1) subject; (2) sex; (3) social context (M-A, M-M, M-RF, M-RF/SF); (4) unit durations to the nearest 0.033 s; (5) display type; (6) separation distance (cm) between lizards; (7) position of display, if display was performed in a volley (i.e., successional displays less than 2 s apart with no change in perch position; sensu DeCoursey and Jenssen, 1994); and (8) other non-head-bob movements and behaviors (e.g., body postures [static modifiers] and non-stereotyped movements [dynamic modifiers] associated with the display behavior; Jenssen, 1979).

The durations (s) of display units were analyzed using descriptive statistics (mean \bar{x} , \pm standard error [SE]) and coefficient of variation ($CV = SD * 100/\bar{x}$). The latter quantifies relative stereotypy, where greater stereotypy is indicated by decreasing CV values. As a convention, units with a CV less than 35% are considered highly stereotyped behavior (Barlow, 1977). In computing CV values, a mean value for each subject was used as an individual observation to eliminate bias due to unequal numbers of sample sizes among subjects. Statistics were computed using PC-SAS version 6.08 (SAS Institute Inc., 1989).

RESULTS

Display Behavior - Basic Structure

The displays of both sexes were unusual, as they were composed of many similar head nods of shallow amplitude (2.5 ± 0.9 mm vertical head displacement; Fig. 1) and extremely short duration (0.07-0.1 s). Because a nod duration approached that of a muscle twitch (squamate muscle fibers, 0.025-0.056 s; Guthe, 1981), we used the term 'twitch-nod' to describe a single head nod. The cadence of all displays was defined by 'bursts' of multiple twitch-nods, where the nod rate within bursts was fairly constant (11.6 ± 0.8 nods/s). The duration of twitch-nod bursts ranged from 0.1-1.4 s

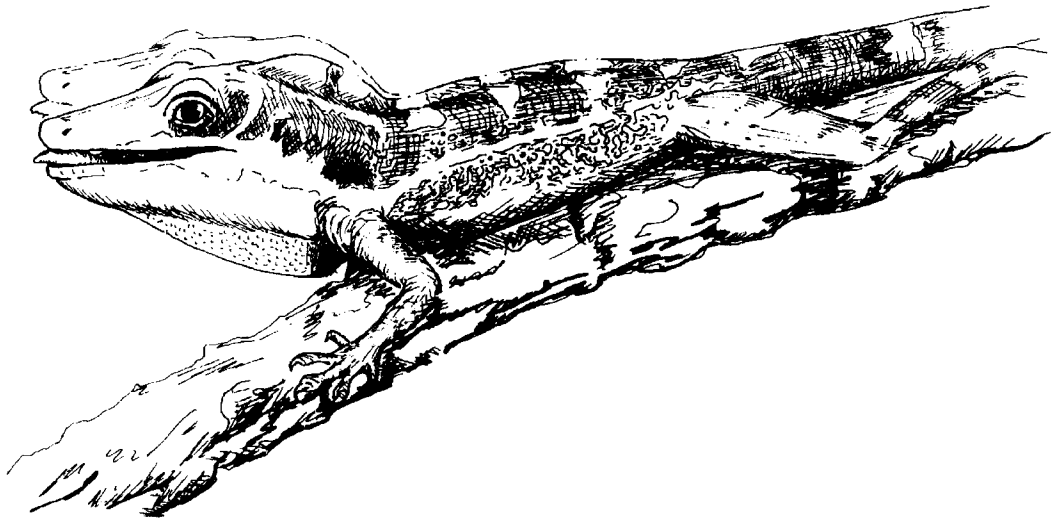


FIG. 1. Male depicting the average amplitude deflection for types A, B and C displays (~2.5 mm), and the following static display modifiers; mouth-gape/tongue-out, lowered hyoid with dewlap extension, raised crest, and lateral compression.

and contained from 1-17 twitch-nods. Bursts of twitch-nods were separated by interburst pauses that were 0.09-1.1 s. Due to their unique display structure, displays were divided for analysis into sequential units based on bursts and interburst pauses, rather than the typical convention which uses headbobs and interbob pauses (e.g., DeCoursey and Jenssen, 1994).

Another unique feature of *Anolis bahoru-coensis* displays was the lack of predictable dewlap movement normally coordinated with anoline displays (Jenssen, 1977; Macedonia and Stamps, 1994). Although the dewlap was extended by both sexes during consensual encounters (M-M and M-RF/SF), it was not pulsed during displays or retracted between displays. Instead, the dewlap was extended in combination with the lowered hyoid and was held in place for large portions of the social encounter. A quantitative analysis of dewlap use was impossible because the diminutive size of the extended dewlap (Fig. 1) could not be followed in many of the lizard head angles presented to the observer.

Display Behavior - Description

Three stereotyped display patterns (Types A, B, C; Fig. 2) were identified from

205 DAP-graphed displays. One non-stereotyped behavior (stepbobbing; Fig. 3) was also identified. Four static and three dynamic display modifiers were performed. Both sexes exhibited all three display types and all seven display modifiers. Only males stepbobbed and used a lateral body presentation during displays.

Type A display.—The 78 Type A displays (65 by seven males, 13 by three females) were composed of a maximum of 65 units for males and 29 units for females ($\bar{x} = 10.46 \pm 0.46$ [SE] s with 31 ± 1.33 display units; Fig. 2). The 'core' of Type A displays included units 1-15 (i.e., every display contained at least 15 units; sensu Jenssen, 1977). The number of units after unit 15 was variable and the length of Type A displays ranged from 5.4-20.2 s in total duration. CV values for Type A displays indicated extreme stereotypy: the core duration CV = 12.7% ($\bar{x} = 5.47 \pm 0.08$ s), with ranges from 1.1-36.1% for individual unit durations 1-21 (Orrell, 1994).

Type B display.—The 99 Type B displays (98 by seven males, one by a female) were short ($\bar{x} = 1.21 \pm 0.06$ s, range of 0.23-3.04 s) and composed of only 4.0 ± 0.22 average display units (range of 1-9; Fig. 2). Although the total number of units in Type B displays was variable, the CV values of

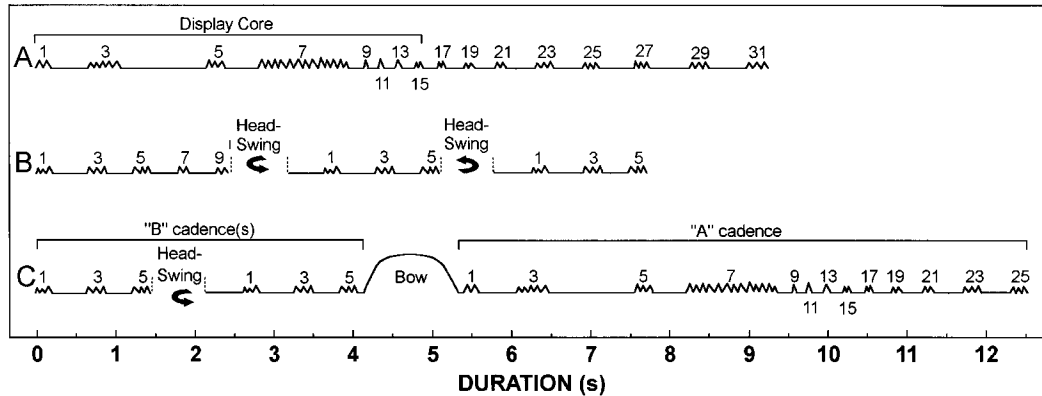


FIG. 2. Display-Action-Pattern (DAP) graphs for male display patterns. Odd numbers indicate units of twitch-nod bursts, even numbered interburst pause units are not labeled. The core of Type A displays (A) included units 1-15 (e.g., units 1-15 were performed in every display) (based on 78 displays performed by ten subjects). Type B displays (B) are presented as a volley of three successive displays separated by headswings (based on 99 displays performed by eight subjects). Type C displays (C) were composed of one or more B cadence patterns separated by a headswing, followed by a bow, then finished with a single A cadence pattern (based on 28 displays performed by seven subjects). The relative amplitude of vertical head displacement is shown in Fig. 1.

individual units 1-9 ranged from 3.9-35.0%, indicating extreme stereotypy (Orrell, 1994). Males performed headswing display modifiers (described below) between the type B displays within 28 of the 31 recorded volleys (Fig. 2) and following eight of the 24 single type B displays.

Type C display.—The 28 Type C displays (26 by six males, two by a female) began with 1-4 repetitions of the Type B cadence pattern (with repeated Type B patterns separated by headswings), followed by 1-3 bows (described below), then concluded with a single Type A cadence pattern (Fig. 2). Comparison of the A and B cadence patterns within the Type C displays with individual Type A and B displays showed that they were very similar; of the 30 homologous units compared (units 1-21 of Type A, units 1-9 of Type B), only one unit differed significantly (Wilcoxon rank-sum, $df = 1$, $p = 0.03$). Because of the variable length of the A and B cadence patterns, the duration of Type C displays (including headswings) had a large range of 6.93-13.99 s ($\bar{x} = 10.85 \pm 0.36$ s). Bows performed within Type C displays added an additional 3.22 ± 0.23 s (1.06-5.40 s) to the total display duration.

Stepbobbing.—Stepbobbing ($n = 5$) involved a quick vertical amplitude shift (10-12 mm) of the head, followed by a 2-11 s pause before the head was again shifted

in the opposite direction (Fig. 3). Sequences of alternating head amplitude ranged from 2-11 in number, with a 19-93 s range in total duration. Although the head positions in stepbobbing were predictable, the durations were not obviously stereotypical. Statistics were not computed for stepbobbing behaviors due to the small sample size.

Static Display Modifiers.—*Anolis bahorucoensis* performed four static display modifiers common to anolines (e.g., Jenssen, 1979): mouth-gape/tongue-out (mouth gaped open and tongue bunched toward or protruded from the front of the mouth), lowered hyoid (throat region enlarged by the lowering of hyoid apparatus), raised crest (erected skin folds along the dorsal midline along the back of the head [nuchal crest] and body [dorsal crest]), and lateral compression of the body (Fig. 1). Performed during conspecific encounters, the effect of static modifiers is to increase the lateral surface area of the displayer as viewed by an opponent (Jenssen, 1979).

Dynamic Display modifier.—Of the three dynamic display modifiers performed, only the bow (gradual high amplitude raising and lowering of the head) has been described for other anoles (e.g., Jenssen, 1979). Two other kinds of movements were performed in association with displays, labeled as the hipkick and the headswing.

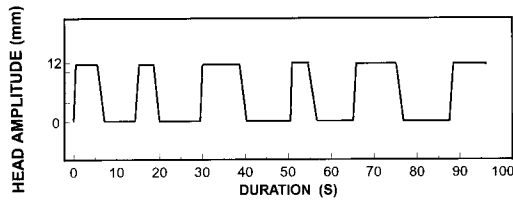


FIG. 3. Stepbobbing head movements performed by males (based on five sequences of stepbobbing behaviors) (relative head amplitude 10-12 mm).

The hipkick is a quick movement ($\bar{x} = 0.6$ s) in which the pelvis and tail are elevated by one rear leg pushing off the substrate while the rear leg nearest the displayer's opponent is lifted from the substrate; the amplitude of movement varied from a slight jump of a few millimeters in height to both rear legs being thrust off the perch. From 2-6 hipkicks were performed in quick succession. All males and one female performed hipkicks ($n = 86$), which were executed prior to bows and Type A displays during consensual encounters (Fig. 4).

The headswing dynamic modifier ($n = 32$) is a smooth motion composed of three changes in head position: first, a downward swing of the head to the right or left; next, a swing of the head to the opposite side maintaining the lowered position of the head; last, a raising of the head back to the center starting position. Headswings were also composed of just the downward motion of the head to the right or left ($n = 25$). Headswings were performed by males in conjunction with 68% of B and 85% of C display types (Fig. 1).

Lateral presentation.—Lateral body presentation, a common behavior among anoles (Jenssen, 1979), was performed only by males during consensual encounters ($n = 72$).

Display Behavior - Use

M-A Context.—During eight observation hours the seven solitary males stepbobbled only once and performed just three A, two B, and two C displays for an extremely low combined display rate of 1.1 displays/h. The only display modifiers performed were two headswings and two bows, which were associated with the Type C displays.

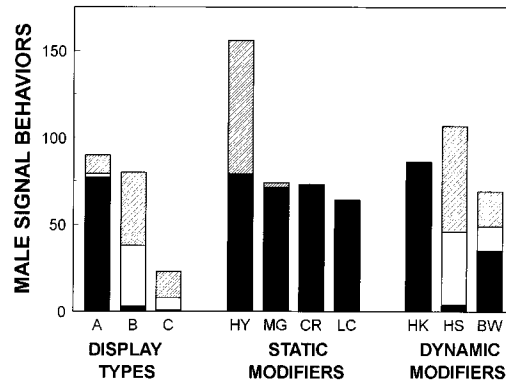


FIG. 4. Number of signal behaviors performed by male *Anolis bahorucoensis* during male-male (■), male-female resident (□) and male-female with strange female (▨) social contexts. Key to modifiers: HY-lowered hyoid, MG-mouth-gape/tongue-out, CR-raised crest, LC-lateral compression, HK-hipkick, HS-headswing, and BW-bow.

M-M Context.—Type A displays, static modifiers, and hipkicks were the predominant signals performed in this context (Fig. 4). Ninety percent of displays performed in the M-M context were Type A displays. Together, Type B and C patterns composed only 5% of displays performed, and stepbobbing the other 5%. All displays performed in M-M context were single displays; no displays were given in volleys. The combined average display rate for M-M context was four-fold that of the M-A context, yet was still only 4.5 displays/h.

Males employed static modifiers in a progressive manner typical of anoles (Jenssen, 1979; Losos, 1985b), combining two or more modifiers as encounters became more aggressive. Lowered hyoid was the first modifier performed and had the highest frequency (\bar{x} rate = 5/h). Mouth-gape/tongue-out was the next modifier to appear (\bar{x} rate = 4.6/h), followed by raised crest and lateral compression (\bar{x} rates = 4.2 and 4.1/h, respectively). Lateral presentation was used to position the displayer at a right angle to the opponent just prior to performing hipkicks (\bar{x} rates = 3.9 and 4.8/h, respectively), which were followed by 1-2 bows (\bar{x} rate = 2/h), then a Type A display. Lateral presentation prefaced 93% of the Type A displays.

The 12 intermale encounters terminated at one of four levels of aggression: no signalling or overt interaction ($n = 1$); displays and modifiers only ($n = 4$); pursuit/fleeing or hiding with no physical contact ($n = 4$); and, pursuit/fleeing after a biting attack ($n = 3$). The flight of the 'loser' determined a 'winner' in only the last two levels of encounters. Of the seven winners, three were intruders (i.e., crossed into their opponent's home area) and four were 'residents' (i.e., remained in their home area). Six of the seven winners were larger than their opponents. The one smaller winner was also a resident.

M-RF Context.—Type B (79%) and C (18%) displays were the predominant signals performed by males in this context (Fig. 4), with most of the Type B displays (73%) given in volleys. Mean male display rate for all display types combined (15.7 displays/h) was three times that of M-M context (4.5 displays/h). The only modifiers males performed were headswings and bows associated with B and C display types (\bar{x} rates = 9.6/h and 1/h, respectively; Fig. 4).

Females performed only two type A displays, making the female mean display rate during the M-RF context the lowest of any context at 0.46 displays/h. The only display modifier females performed in this context was a single bow. Despite the low signalling rates, females were known to be reproductive based on two observed copulations (\bar{x} duration = 3.9 min) and the laying of viable eggs.

M-RF/SF Context.—As in the M-RF context, males performed mostly Type B and C displays (Fig. 4), with about the same percentage of B displays given in volleys (74%). At 19.6 displays/h, the M-RF/SF context had the highest average display rate of any context. Bows and headswings were performed in association with the Type B and C displays (\bar{x} rates = 4 and 6/h, respectively). Males also performed lowered hyoid (\bar{x} rate = 4/h), two incidences each of lateral compression and lateral presentation, and one incidence each of raised crest and mouth gape (all \bar{x} rates less than 0.1/h). The higher display rate and lowered hyoid probably indicated the males'

aroused interest in a new mating opportunity; yet a male pursued a strange female only once.

Strange and resident females in the M-RF/SF context performed 14 Type A displays, one B and two C displays for a combined mean rate of 1.9 displays/h. Females used static modifiers in a similar manner as males during the M-M context, except that mouth-gape/tongue-out was the most frequent modifier (\bar{x} rate = 11.7/h), followed by lowered hyoid (\bar{x} rate = 2.3/h). Lateral compression and crest were used infrequently (\bar{x} rate less than 1/h). Bows were performed by the three females in association with Type A displays (\bar{x} rate = 1.7/h), but only one female performed hipkicks ($n = 2$; \bar{x} rate less than 1/h). Only one incident occurred in which a strange female was chased by a resident female. No copulations or indications of female receptivity were observed during the M-RF/SF context.

Separation Distance.—For all social contexts, there was a consistent trend for displays (63% for males, 85% for females) and display modifiers (83% for males, 100% for females) to be used most frequently when subjects were less than 40 cm apart. Only 22% of displays and 6% of modifiers were performed at long (greater than 80 cm) separation distances. The lowered hyoid, headswing, and bow were the only modifiers males performed at more than 80 cm.

DISCUSSION

Comparison to other Anoles

Several aspects of this species' display behavior are similar to those of other anoles. These include a multiple display repertoire of species-specific and stereotyped headbob patterns (e.g., Hover and Jenssen, 1976; Jenssen and Rothblum, 1977; Jenssen and Gladson, 1984), shared by both females and males (Jenssen, 1971; Stamps, 1973), and a repertoire of typical display modifiers (Jenssen, 1979). Hipkick and stepbobbing are also similar to behaviors described for other anoles (Gorman, 1968; Jenssen, 1979; Losos, 1985b). Although the headswing bears a resemblance to 'lateral

head movements' described by Font and Kramer (1989), this behavior may be species-unique.

Finally, as with other anolines (e.g., Hover and Jenssen, 1976; Jenssen, 1979; Bels, 1986), *Anolis bahorucoensis* display types and modifiers appear to have specific functions as inferred from their differential use across social contexts (Fig. 4). Type A displays, static modifiers, and hipkicks were performed mainly during consensual encounters and may have agonistic functions. Type B and C displays and associated headswings were performed mainly during male-female contexts and may function in courtship.

Anolis bahorucoensis exhibits four departures from typical anoline display behavior. First, the extremely low amplitude and rapid frequency of twitch-nods are 2-3 times lower in amplitude and a tenth of the duration of typical headbobs of anoline displays (e.g., Stamps and Barlow, 1973; Jensen, 1977; Fleishman, 1992). Although similar low amplitude and rapid frequency head movements have been described for other anoles (e.g., Scott, 1984; Queral et al., 1995), they differ in that they are not known to make up the stereotypic cadence patterns that define the species' display types.

Second, the display design was also unusual in that dewlap pulsing, or dewlap extension and retraction, was not coordinated with the display patterns (e.g., Jensen, 1977; Macedonia and Stamps, 1994). When males used their diminutive dewlap, it was not retracted during or between individual displays. The dewlap was simply held in an extended position in combination with the lowered hyoid. In this respect, the dewlap functioned as a static display modifier by increasing the displayer's lateral surface area.

Third, both sexes demonstrated very low display rates during all social contexts as compared to most anoles (e.g., Williams and Rand, 1977; Stamps, 1983; DeCourcy and Jenssen, 1994). During the M-A context, males averaged about one display/h. Although captivity may have suppressed their behavior, infrequent M-A displays suggests that displays are little used to

advertise territorial residency. The M-M context display rate was only 4.5 displays/h, about 3% of the 144 displays/h that *A. carolinensis* performed during the same context and under the same experimental protocol (DeCourcy and Jenssen, 1994). Male display rates during the M-RF and M-RF/SF contexts (15.7 and 19.6 displays/h, respectively) were four times higher than the intermale display rates. Males seemed more interested in displaying to females than in defending their personal distance or cage 'territory' from other males.

Fourth, intermale encounters demonstrated none of the ritualized behaviors of circling, jaw-sparring, and jaw locking reported for many anoles (Rand, 1967; Jenssen et al., 1984; Losos, 1985b). In anoles where male aggression is intense and determines control of breeding territories, ritualized combat is prominently exhibited, presumably as a forum to assess fighting prowess and to avoid debilitating injury (e.g., Parker, 1974; Jenssen, 1983). Low display rates, nonritualized combat, and little escalated aggression suggest that male *A. bahorucoensis* do not engage in frequent or intense intermale combat for territories.

Functional Consequences

The atypically small dewlap of *A. bahorucoensis* is consistent with the other display parameters: extremely low headbob amplitude, lack of dewlap extension with displays, and infrequent display performance. All de-emphasize display conspicuousness. First, amplitude limits the distance from which conspecifics can detect displays. The 15 mm-amplitude displays of *Anolis auratus* should be perceived by conspecifics up to a distance of about 4.5 m (based on Fleishman, 1992). Assuming that their visual system is similar, the low amplitude displays of *A. bahorucoensis* would transmit at a distance of only 0.3-1.1 m. Second, in most anoles the large extended dewlap with contrasting brightness and UV reflectance (Fleishman et al., 1993) is pulsed or extended during a display, providing an effective leading edge to facilitate motion detection of displays across long distances and against the back-

ground movement of vegetation (Fleishman, 1992). The design of *A. bahorucoensis* displays, therefore, seems to limit signal transmission distance. This interpretation is supported by the tendency of the species to use signals at close (less than 40 cm) inter-subject separation distances.

Short transmission distance displays implies that social interactions are limited to conspecifics within a close proximity. With the small home-ranges suggested for *A. bahorucoensis* males and females (1.5 m² and 2.3 m², respectively; Fitch and Henderson, 1987), conspecific neighbors could be distributed within the 0.3-1.1 m estimated transmission distance of displays. Anoles in populations with high density (Philibosian, 1975; Schoener and Schoener, 1982) or those clumped into limited or preferred habitat (Rand, 1967) may have conspecific neighbors within close distances, but there are no published estimates of population distribution for *A. bahorucoensis*. In addition, if conspecifics were distributed in close proximity, one would expect a higher frequency of display interactions (Ruibal and Philibosian, 1974; Lister and Aguayo, 1992), not the infrequent displays that we observed.

Adaptive Hypotheses

The qualities of *A. bahorucoensis* display structure and use seem paradoxical; perhaps they reflect a tradeoff between strong but countering selection pressures. On the one hand, the species fits the usual pattern for anoline display behavior in which specific visual displays are predictably associated with reproductively important interactions. It seems that positive selection for the maintenance of these communication signals results from the activities in which the display behaviors function. On the other hand, display design and infrequent use of displays are opposite to that expected of highly visible, socially important signals. This suggests a strong penalty if the displayer is too conspicuous. In seeking an explanation for the evolution of *A. bahorucoensis* display behavior, we examine three hypotheses: habitat constraint (e.g., Endler, 1992), social structure (e.g., Rand et

al., 1975), and predator exploitation (e.g., Endler, 1987).

Habitat.—*Anolis bahorucoensis* habitat is characterized by dense vegetation and dim light (Fitch and Henderson, 1987; Orrell, 1994), conditions that could render visual displays difficult to see (Jenssen and Swenson, 1974; Stamps, 1977; Endler, 1992). For headbob displays to be effective in this environment, one would predict that selection would favor high amplitude headbobs that would stand out against the background movement of vegetation (Fleishman, 1988b, 1992) and minimize signal degradation (Endler, 1992). Since the ability of the visual system to track fast-moving objects decreases at lower light intensity (e.g., flicker-fusion frequency; Jenssen and Swenson, 1974), one might also predict that the velocity of visual displays performed in a forest habitat would be slower than those performed in brighter light intensities (Endler, 1992). In addition, the dewlap would be most effective in facilitating signal transmission if colored yellow or yellow-green to provide maximum reflectance of the yellow-green wavelengths that dominate forest shade (Endler, 1992; Fleishman, 1992), and if it were extended or pulsed during the display to provide a conspicuous leading edge for motion detection (Fleishman, 1992).

Clearly, *A. bahorucoensis*' extremely low amplitude and rapid frequency twitch-nod displays are not consistent with the above expectations. Even though the dewlap is predominantly yellow-green as predicted, its diminutive size and infrequent extension contradict an important role in conspecific display detection. It seems that the inconspicuous displays and dewlap would be even less detectable in the species' visually constrained habitat. Although difficult to detect signals could lead to diminished function and relax the selection that maintained displays, *A. bahorucoensis* displays still seem to serve important social functions. We therefore reject the hypothesis that selection pressures due to habitat constraints caused the atypical display traits and reduction in dewlap size.

Social Structure.—Anoline display behaviors are functional units that coordinate the

social structure and mating system of a species. Many anoles practice territory-defense polygyny (Stamps, 1983). In this social context male display behavior would be selected for conspicuous and long distance territorial advertisement (Stamps and Barlow, 1973; Endler, 1992; DeCoursey and Jenssen, 1994) and for frequent use in advertisement, defense, and courtship (Stamps, 1977). The frequent territorial defense associated with a polygynous mating system would select for ritualized aggression to reduce the occurrence of injury. To encompass the home-ranges of more than one reproductive female, it is also expected that polygynous males would defend a large home-range (Stamps, 1983; Nuez et al., 1997).

The display behavior of *A. bahorucoensis* seems poorly adapted for maintaining large exclusive territories. The short transmission distance of the displays would be ineffective for territorial advertisement. The absence of M-A displays may indicate that males avoid a prime means to advertise their presence in a territory. Further, *A. bahorucoensis* exhibited inconsistent and nonritualized intermale aggression, which would normally preserve their mating rights to resident females. Finally, it is unlikely that the reported 1.5 m² home-range of a male would provide exclusive access to more than one female, especially if females have larger (2.5 m²) home-ranges than males (Fitch and Henderson, 1987).

Male display behavior in the lab suggests that *A. bahorucoensis* does not practice territory-defense polygyny. The species' extreme sexual dimorphism, both in size and coloration, may indicate another means of intermale competition for mates. Although male-larger sexual size dimorphism is an anoline trait typically associated with intermale competition (Stamps, 1983), sexual size and epigamic dimorphism could also be associated with female choice (O'Donald, 1983). In fact, the highest male display rates and most complex signal repertoire (Fig. 4) occurred during encounters with females—a possible indication that display function in courtship is more important to male reproductive success than territorial advertisement and defense.

Although there is no evidence to suggest that social structure has contributed to reduced display conspicuousness and dewlap size, it is possible that short display transmission distance places limits on social structure.

Predation.—Because the typical display movements and dewlaps of anoles are designed to be conspicuous, they are also likely to draw the attention of predators (Fleishman, 1992; Endler, 1992; Reagan and Waide, 1996). Since all anolines are subject to predation, the rarity of dewlap size reduction would tend to contradict predation as a causative selective pressure. However, some anoles eat lizards (Fitch and Henderson, 1987), and with a visual system attuned to detect headbob display and dewlap movement (Fleishman, 1992) they present a considerable threat. As one of the smallest of about 18 species in its range (Schwartz and Henderson, 1991), *A. bahorucoensis* is a likely target for congeneric predation. Much larger in size, *A. cybotes* and *A. coelestinus* (\bar{x} SVL = 75 and 60 mm, respectively; Fitch and Henderson, 1987) are abundant within the habitat, and readily attack and eat even adult male *A. bahorucoensis* (Fitch and Henderson, 1987).

The atypical display behavior of *A. bahorucoensis* seems to fit the profile of a species subject to intense visual predation. Small dewlaps that are inconspicuous even when extended, and the low amplitude twitch-nods, may be signals which can be detected by conspecifics nearby, yet degrade rapidly and are less likely to be detected by anoles at greater distances (Endler, 1992). Exposure to predation would also be minimized if displays were used infrequently, or in conditions of heavy vegetation and deep shade that provided shelter from visually-oriented predators (Endler, 1992). Species adapted to shade or dim light may be able to perceive displays in that environment more easily than predators adapted to brighter conditions (Jenssen and Swenson, 1974). This may explain the low display rates performed by *A. bahorucoensis* in the laboratory and why lizards hid under bright lights.

In conclusion, *A. bahorucoensis* seems to possess a combination of unusual display

traits; the species' highly stereotypic signals seem to fulfill important social functions, yet have a minimized conspicuousness and short transmission distance that contradict normal functions for anoline displays. Our provisional interpretation offers the predation hypothesis as the most likely explanation for the apparent repression of dewlap and display expression in *A. bahorucoensis*. We predict that a field investigation of *A. bahorucoensis* will document a much altered social organization due to display constraints and the threat of predation.

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