

Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*

KRISTI R. DECOURCY & THOMAS A. JENSSEN

Biology Department, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, U.S.A.

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Abstract. *Anolis carolinensis* was found to have three stereotyped and distinct headbob patterns, referred to as types A, B and C. Each type had two variants, one in which the dewlap appeared mid-display, and a second in which dewlap extension was absent. Display types A, B and C comprised all of the headbob signalling during two contexts: (1) the advertisement context, when males were isolated (male-alone); and (2) the aggressive context, when each male was paired (male–male) during territorial contests. During the advertisement context, the mean display rate was 0.3/min; half of the displays were performed singly, the rest in bursts (volleys) of two to six displays/volley. Dewlap extension accompanied 97% of the displays, and all three types of displays were used with similar frequency. During the male–male context, mean display rate varied inversely with inter-male separation distance, being 1.4, 2.0 and 3.8/min at distances greater than 100 cm, within 20–100 cm and less than 20 cm, respectively. At large inter-male separation distances (> 60 cm), long volleys (containing four to nine displays) were common, type C displays predominated, and dewlap extension accompanied 92% of the displays. At short inter-male separation distances (< 20 cm), single displays predominated, the volleys performed had fewer displays, display types A, B and C were performed with similar frequency, and only 7% of the displays had dewlap extension. These results are compared with previously published descriptions of male *A. carolinensis* headbob display behaviour. Recommendations are made for the abandonment of functional labels on patterns of display behaviour (e.g. assertion display and challenge display), regardless of taxon studied.

The green anole, *Anolis carolinensis* Voigt, of the southeastern United States (Conant 1975) is a commonly used reptile for experimental studies, and is perhaps the most studied of lizard species (Crews 1977). Many investigations have focused on the species' ecology, behaviour, endocrinology, and nervous system (e.g. Greenberg & Noble 1944; Gordon 1956; King 1966; Cooper 1977; Greenberg 1977; Crews 1978, 1980; Sigmund 1983; Greenberg et al. 1984; Ruby 1984; Andrews 1985; Greenberg & Crews 1990). Frequently, these studies either associated the display behaviour of *A. carolinensis* with other variables, or the behavioural displays themselves were a primary objective of the study. Despite the plethora of references to the display behaviour of *A. carolinensis*, an accurate characterization of the species' headbob signals has proven elusive.

Beyond the anecdotes of Monks (1881) and Barbour (1926), one of the first descriptions of display behaviour for *A. carolinensis* was by Greenberg & Noble (1944). They noted that the

headbob/dewlap display appeared to be stereotyped, with headbobs 'consisting of five complete up-and-down swings'. Gordon (1956) also referred to a series of five bobs that lasted 1–3 s. Subsequently, McCardell (1971), Crews (1975), Sigmund (1978) and Bels & Goosse (1987) have made more systematic attempts to describe the headbob signals of *A. carolinensis*. Yet procedural or conceptual problems have prevented an adequate resolution of the *A. carolinensis* display behaviour.

To initiate a clarification of *A. carolinensis* headbob signals, we limited our study to adult males within two laboratory-controlled contexts, advertisement and inter-male territorial conflict. The study had three objectives. (1) to select equipment and protocol to produce a video record of display behaviour in which the display characteristics would approximate those of free-ranging males; (2) to ascertain and describe the number and structure of the headbob signals performed during the two

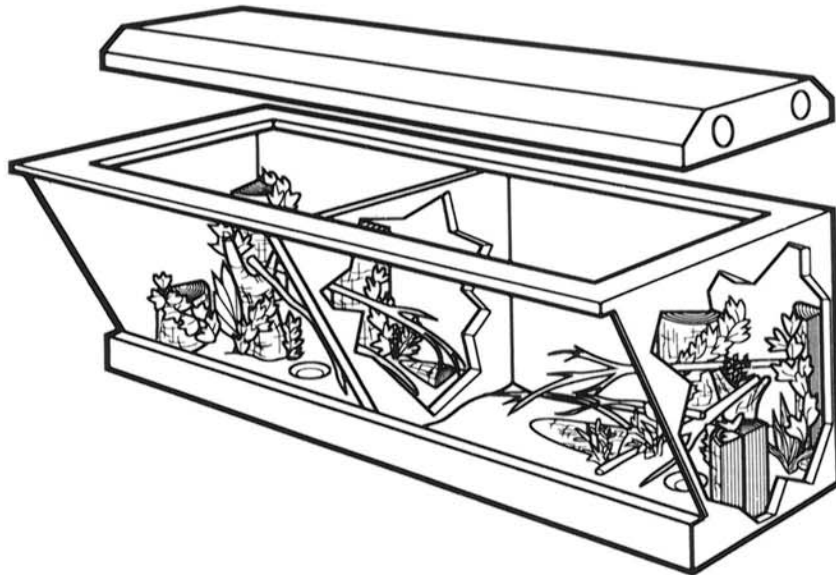


Figure 1. Cutaway diagram of the observation chamber showing slanted glass front, removable partition, fluorescent lighting, and habitat configuration. Not shown is the spotlight at each end of the chamber.

contexts; and (3) to indicate how the different headbob signals are used within the given contexts. Because of the complexities of the present analysis, aggressive signals other than headbobs will be addressed elsewhere. These include colour and postural changes (e.g. 'modifiers', sensu Jenssen 1979) which are very similar in form among anolines (Jenssen 1977) and have been previously described for *A. carolinensis* (Greenberg 1977).

METHODS

We collected adult *A. carolinensis* males ($\bar{X} \pm (SE)$ snout-vent length (SVL) = 60.8 ± 0.44 mm; mean weight = 5.2 ± 0.10 g) in Palatka, Florida, and transported them to the behaviour laboratory at Virginia Polytechnic Institute and State University. Anoles were toe-clipped for individual identification. No subject was kept for longer than 3 months. While in the laboratory, each male was housed separately with a female in $0.6 \times 0.6 \times 0.7$ m glass-fronted wooden enclosures, having no visual contact with male conspecifics. All cages had a substrate of peat moss and simulated habitat of branches and artificial vegetation. Cages were

under fluorescent and incandescent lighting on a 14:10 h light:dark cycle, a lighting regimen known to maintain gonadal recrudescence in *A. carolinensis* (Licht 1971). Cage temperature was about 24°C at night, with a gradient during the day from 30°C to 35°C at perches directly under incandescent bulbs. Water was available in shallow bowls embedded in the substrate and as droplets from daily misting. Lizards were fed daily on crickets dusted with powdered calcium lactate.

We videotaped each of 40 males alone (male-alone advertisement context) and when paired with another male (male-male aggressive context). The following protocol for these observations attempted to: (1) minimize handling and observer effects (sensu Altmann 1974); (2) establish the desired social context and subject motivational state; and (3) provide a spatial-habitat setting that was larger and more realistic than usually employed in laboratory investigations.

We moved subjects two at a time into a $2.4 \times 0.6 \times 0.8$ m observation chamber which was fitted with a slanted glass front to prevent the subjects from seeing and displaying at their own reflections (Fig. 1). The paired subjects, one of which was marked with a white acrylic dot on its tail, were

separated by an opaque removable partition that bisected the chamber. This created the male-alone context.

We constructed duplicate habitats on each side of the partition and arranged the lights and physical structures to encourage initial maximum inter-male separation distances, while minimizing blind spots during videotaping. We fitted vertical tree bases (halved or quartered) flush against the walls and corner at opposite ends of the chamber, with the majority of artificial vegetation and the focus of spotlamps at these locations. Horizontal branches, positioned highest at the rear of the chamber and lowest toward the front, radiated from each habitat cluster towards the central partition (Fig. 1). This provided predictable routes of approach should one subject decide to invade the other's habitat when the divider was removed.

All observations and videotapes were made from a separate room through a small glass viewing window 1.5 m from the event chamber; this reduced any possible observer effect (Sugarman 1990).

We did not use an arbitrary, fixed 'acclimation' period before making our observations. Because we wanted to examine the kinds of headbob signals and their manner of employment during territorial confrontations, it was important that the subjects indicated to us when they had acquired a territorial motivational state. Two subject-determined criteria were used: (1) non-directed advertisement displaying, while (2) moving (i.e. patrolling) within their habitat. These criteria, for example, would not be met if a male were to display at his own reflection while in a glass-walled terrarium (not an advertisement context) or if his movements were escape-motivated wall climbing. Depending on the subject, 4-7 days were required to meet the two criteria, at which time we videotaped the behaviour of each solitary male for 30 min using the same equipment as listed below.

We created the male-male context by removing the central partition. At this moment, subjects had the choice to invade the other's habitat or to co-exist; all encounters produced a male who chose to invade. The ensuing behaviour was videotaped until one male clearly demonstrated flight behaviour (i.e. continuously fleeing and hiding in the habitat in response to the other male); this took 12-68 min.

To make a detailed behavioural analysis of the pair, we used two telephoto video-cameras and followed each male with a separate camera. The two

camera images were juxtaposed onto the videotape (Vicon Model V270SP split screen generator) and elapsed time (Odetics Model G-77 time-date generator) superimposed in 0.01-s increments. The audio track of the videotape was used to record subject data, observational notes, and estimated inter-male separation distances each time the subjects moved. Determining the latter was facilitated by a metric tape fixed along the bottom front of the chamber. We used a Panasonic (Model AG-1950) videocassette recorder, with a resolution of 30 frames/s, for recording and frame-by-frame playback.

We determined the occurrence, frequency and duration of four classes of potential signals (locomotion, body colour, postures and headbob patterns) from the videotapes. However, only one class (headbobs) is analysed here. To do this, we generated Display-Action-Pattern (DAP) graphs (sensu Carpenter 1965) from a video-monitor using frame-by-frame measurements. The vertical position of the head in each frame was calculated using a digitizer (Numonics Model 274-167); this quantification of head amplitude position (Y -axis) was then graphed against time (X -axis) in 0.033-s increments. Each DAP graph was divided into naturally occurring 'units' (sensu criteria of Drummond 1982), where each unit was either a headbob or an inter-bob pause. Durations (to the nearest 0.033 s) were recorded for each headbob (i.e. temporal difference between initial upward movement of the head to end of downward movement) and each inter-bob pause (i.e. temporal difference between end and beginning of successive bobs).

We DAP-graphed a total of 190 male-alone displays and 194 male-male displays. We determined the number of different headbob patterns (i.e. 'display types', sensu Jenssen 1978) from the DAP-graphs from both contexts. Once the DAP-graph technique had revealed the various display types, we typed an additional 1810 male-male headbob displays without DAP-graphing.

Headbob displays occurred singly or as two to nine consecutive displays in a burst, termed a 'volley'. We considered displays separated by less than 2 s as being part of a volley; longer separation times defined solitary displays. Subjects always maintained their perch position while displaying singly or in a volley.

We recorded the following data for each DAP-graphed display: (1) subject identification; (2) social context (male-alone or male-male); (3) duration of headbob and inter-bob units; (4) presence or

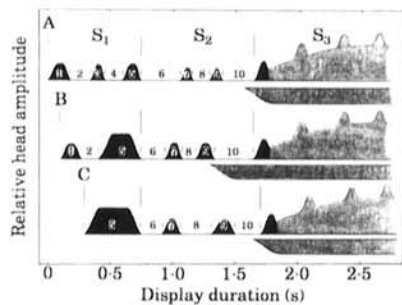


Figure 2. Generalized Display-Action-Pattern graphs from 384 displays by 26 males for the three territorial display types of *A. carolinensis*. The X-axis is elapsed time (s), and the Y-axis is relative vertical amplitude of the head and dewlap, plotted above and below the baseline, respectively, for each display type. Numbers (1–10) indicate display units, and the divisions and the labels (S1, S2 and S3) above each display indicate display sections. The grey portions of the displays (i.e. the dewlap extension and most of the S3 section) were not included in all displays, although all displays had at least one headbob in the S3 section. Unit durations and the number of headbobs in the S3 section were derived from individual means (see Table I).

absence of dewlap extension; (5) if dewlap presented, unit of emergence; (6) display type; (7) duration of the S3 section (see Fig. 2); (8) number of headbobs in the S3 section (see Fig. 2); (9) position, if display were a part of a volley (e.g. first, second, etc.); (10) total number of displays in the volley; and (11) inter-male separation distance. For displays not DAP-graphed, variables 3, 5, 7 and 8 were not determined. Data were analysed using statistical procedures from the SAS (SAS Institute 1985a, b, c) and Siegel (1956). Means are presented \pm SE. Means were considered significantly different if $P < 0.05$. Non-parametric tests were used when possible.

To eliminate bias due to unequal numbers of displays for each individual, we used intra-subject means for display variables as single observations in all analyses except where sample size bias by subject was not a concern, as in: (1) nearest neighbour discriminant analysis to determine the number of the 384 displays that had been mis-typed; (2) canonical discriminant analyses to examine relative separation among display types; and (3) nested analysis of variance (ANOVA) to determine the source of the variation in the unit durations.

RESULTS

Display Description

Display types

The 384 DAP-graphs revealed that three stereotyped headbob patterns, labelled display types A, B and C (Fig. 2), were performed in both male-alone and male-male contexts. All three display types were composed of three similar sections. Referring to Fig. 2, the first section (S1) contained one to three headbobs and zero to two inter-bob pauses, depending on display type. The second section (S2) consisted of two bobs and three inter-bob pauses for all three display types. The third section (S3) contained one to nine shallow headbobs superimposed on a rising head amplitude for all three display types.

Numbering of the units followed perceived homologies between display types. Display types A, B and C all shared the same headbob organization for sections S2 and S3 (Fig. 2). Therefore, units in these two sections were considered to be homologous between display types and were given the same corresponding number designation. Only the units of the first section (S1) posed a difficulty, because they could vary from five (three bobs and two inter-bob pauses) in the type A display to one (one bob and no inter-bob pause) in the type C display (Fig. 2); thus, some of the S1 units were not represented across display types. The numbering of S1 units followed an assumption of bob fusion (or splitting) during the evolution of the display repertoire; this will be discussed below.

Stereotypy

Descriptive statistics on the unit durations of display types A, B and C quantified the cadence of the bobbing pattern within each display type (Fig. 2; Table I). When units of the same number designation were compared across display types, durations in 14 of the 20 possible comparisons were significantly different (Table II); a few comparisons were perhaps significant by chance alone.

To demonstrate that the display types were easily distinguishable, we analysed the data using a nearest neighbour discriminant analysis (SAS). Based on the durations of units 1–10, the test calculated a discriminant score for each observation and then used the score to assign the observation to the display type for which it had the greatest probability of

Table I. Descriptive statistics for headbob unit durations of the three territorial display types of male *A. carolinensis*, based on individual means for type A displays by 17 males, type B displays by 21 males, and type C displays by 22 males

Display	Unit	Pooled			Male-alone		Male-male	
		Mean (s)	SE	CV	Mean (s)	SE	Mean (s)	SE
Type A	U1	0.192	0.017	37.3	0.221	0.042	0.180	0.184
	U2	0.174	0.025	59.2	0.190	0.055	0.155	0.150
	U3	0.119	0.006	21.5	0.129	0.018	0.118	0.122
	U4	0.158	0.013	33.3	0.139	0.024	0.162	0.160
	U5	0.142	0.011	31.5	0.174	0.018	0.126	0.126
	U6	0.320	0.013	17.0	0.302	0.021	0.332	0.328
	U7	0.104	0.005	18.6	0.112	0.012	0.102	0.104
	U8	0.138	0.008	22.9	0.136	0.018	0.134	0.135
	U9	0.105	0.004	17.2	0.117	0.012	0.101	0.102
	U10	0.238	0.014	25.0	0.249	0.021	0.231	0.220
Type B	U1	0.152	0.012	35.9	0.183	0.022	0.138	0.009
	U2	0.172	0.021	56.0	0.162	0.045	0.183	0.016
	U5	0.322	0.012	17.0	0.337	0.024	0.315	0.010
	U6	0.221	0.014	28.1	0.190	0.017	0.223	0.017
	U7	0.125	0.009	31.8	0.149	0.017	0.116	0.006
	U8	0.128	0.012	43.6	0.106	0.021	0.127	0.012
Type C	U9	0.130	0.008	27.5	0.148	0.017	0.125	0.005
	U10	0.317	0.019	27.5	0.286	0.027	0.337	0.021
	U5	0.436	0.015	16.1	0.447	0.019	0.444	0.019
	U6	0.188	0.019	46.5	0.211	0.034	0.180	0.012
	U7	0.133	0.008	29.0	0.147	0.013	0.131	0.012
	U8	0.247	0.010	19.8	0.244	0.018	0.245	0.014
	U9	0.173	0.010	27.1	0.175	0.015	0.180	0.012
	U10	0.221	0.011	23.9	0.220	0.021	0.211	0.011

Table II. Wilcoxon rank-sum tests for differences in unit durations between the territorial display types of male *A. carolinensis*. Display types were paired for comparisons; display type means were derived from individual means

Units	Type A versus type B		Type A versus type C		Type B versus type C	
	χ^2	$P <$	χ^2	$P <$	χ^2	$P <$
1	6.303	0.0121	—	—	—	—
2	0.235	0.6386	—	—	—	—
5	26.861	0.0001	28.059	0.0001	23.263	0.0001
6	16.061	0.0001	18.779	0.0001	3.591	0.0581
7	3.114	0.0776	5.269	0.0217	0.606	0.4433
8	1.558	0.2121	25.421	0.0001	23.853	0.0001
9	5.471	0.0193	18.925	0.0001	9.011	0.0027
10	8.621	0.0033	0.848	0.3572	14.189	0.0002

$df = 1$ for all tests.

membership. The discriminant analysis placed only three of the 384 displays (0.8%) in a different display type than the one to which it had originally been assigned.

To indicate the extent of separation between display types, a canonical discriminant analysis (SAS) was performed. Canonical correlations were derived from the durations of units 1–10. The first

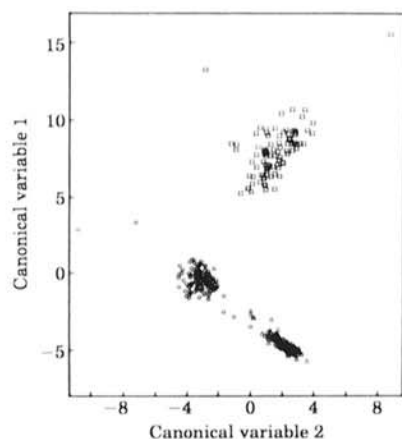


Figure 3. Plots of the first two canonical variables from a discriminant analysis of units 1–10 for 384 territorial displays by 26 male *A. carolinensis* of type A (□), type B (◇) and type C (△) displays.

and second canonical variables were plotted against each other, showing clear separation of display types with no overlap (Fig. 3).

As a measure of relative stereotypy, the coefficient of variation (CV) was calculated for all unit durations. The CV values ranged from 16.1 to 59.2% (Table 1). Behavioural units with a CV of 35% or less reflect highly stereotyped behaviour (Barlow 1968); all but six of the 24 *A. carolinensis* headbob units fell within this range (Table 1).

Source of unit variance

Total display variance was partitioned according to display type, context, between subjects, and within subjects using a nested ANOVA (SAS). Variance for units 1–5 and 8 was primarily due to the display type (Fig. 4). The variance in units 6, 7, 9 and 10 was primarily due to between- and within-subject components (Fig. 4). However, even the most variable unit had a very small standard error (<0.4 s), with the real time variance for any given unit only a fraction of a second (Table 1). Therefore, variance as a source for identifying individual displayers (between-lizard differences) or as an indicator of arousal intensity (within-lizard variation) seemed unlikely. Only a small portion ($\bar{X} = 3.9\%$) of the variance of any unit was due to social context (Fig. 4).

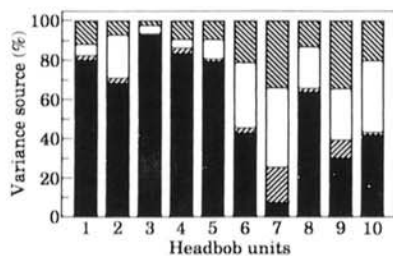


Figure 4. Proportion of variance found in 384 type A, B and C territorial displays by 26 male *A. carolinensis* attributed to type of display (■), context (▨), between-subject (□) and within-subject (⊞) components of a nested ANOVA.

Because previous reports have inferred that *A. carolinensis* displays vary by context (e.g. 'assertion' and 'challenge' displays; see Discussion), we compared each unit duration within each display type across the male-alone and male-male contexts. Almost no differences were found (Table 1). Only one of the 24 units (4.2%) was significantly different (Table 2), and with 24 comparisons, significance would be expected in some tests by chance alone. Therefore, context did not appreciably affect the cadence pattern of the three display types.

Sections compared

The S1 section (consisting of one to three headbobs, depending on display type) contained the primary criteria for discriminating the three display types. The rationale for unit labelling in S1 for type B and C displays rests on the perception that the S1 bob patterns of these display types were derived from those of the S1 section of type A displays. The durations of the first three bobs of the type A displays (units 1+3+5), the first two bobs of the type B displays (units 1+5), and the first bob of the type C display (unit 5) averaged 0.45 ± 0.03 , 0.47 ± 0.02 , and 0.44 ± 0.15 s, respectively; these durations were not significantly different (Kruskal-Wallis test, $\chi^2 = 3.54$, $df = 2$, $P < 0.17$). It is feasible that the progenitor of the three S1 patterns began with the type A pattern and, through progressive fusion of bobs, produced the two other S1 patterns: units 3+5 of type A fused to make unit 5 of type B, and units 1+5 of the type B fused to create unit 5 of type C. The reverse is also a possibility, where the long, initial bob (unit 5) of the type C display separated first into units 1 and 5 (type B) and then again to produce units 1, 3 and 5 (type A).

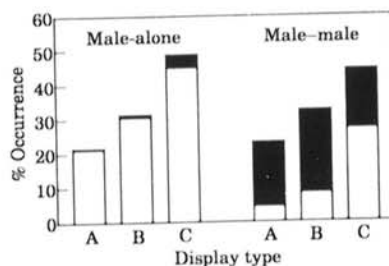


Figure 5. Proportion of three display types performed in the male-alone and male-male context with (□) and without (■) dewlap extension by male *A. carolinensis*, based on 2194 displays by 38 individuals. Proportion of display types used were determined for each male in both contexts, and the individual proportions averaged.

The S2 section, containing two quick bobs (Fig. 2), had an almost identical total duration between type A, B and C displays, being 0.91, 0.92 and 0.96 s, respectively, and exhibited very low CV values (6.8, 12.2 and 10.9%, respectively), indicative of high stereotypy. For all display types, dewlap extension was coordinated with the last units of S2 (Fig. 2).

In the S3 section, the lizard lifted its head to a level equivalent to the height of the previous headbob units while performing a variable number of shallow headbobs (Fig. 2). The S3 bob series varied in number from one to nine, with the amplitude of successive bobs progressively dampening. Based on 132 displays, the S3 duration averaged 1.21 ± 0.07 s. There was no significant difference in S3 duration between the display types (Kruskal-Wallis test, $\chi^2 = 0.30$, $df = 2$, $P < 0.86$). The number of bobs in the S3 section of the display averaged 3.3 ± 0.1 , with no significant difference in the number of bobs between display types (Kruskal-Wallis test, $\chi^2 = 0.98$, $df = 2$, $P < 0.61$). The duration of the S3 section was positively correlated with the number of bobs in the section (Spearman correlation test, $N = 121$, $r = 0.62$, $P < 0.0001$).

Signal Use

Male-alone

Solitary males performed all three display types, with type C display being the most common (Fig. 5). Mean display rate was approximately 0.3 displays/min. Males performed solitary displays 54% of the time. The remaining bouts of displaying were volleys of two to six displays

($\bar{X} = 2.7 \pm 0.1$, $N = 69$ volleys). Dewlap extension accompanied 97% of all male-alone displays (Fig. 5).

The type of display used when displaying singly or in volleys followed some trends. Solitary displays were mostly type A displays (47, 28 and 25%, for types A, B and C, respectively; $N = 53$ displays). The composition of volleys varied by volley length. Short volleys (\leq three displays) contained mostly type B displays (15, 45 and 40%, for types A, B and C, respectively; $N = 86$). Long volleys (\geq four displays) contained mostly type C displays (2, 28 and 70%, for types A, B and C, respectively; $N = 50$). The difference in volley composition for short and long volleys was significant ($\chi^2 = 13.38$, $df = 2$, $P < 0.01$).

Male-male

The male-male display rate was considerably higher than in the male alone context, averaging 2.4 ± 0.21 displays/min. Of the 1982 displays occurring during male-male observations, 1070 were solitary and the rest were distributed between 214 volleys, with displays/volley having a mean of 3.5 ± 0.11 and a range of 2–9.

During male-male encounters, certain features of the display behaviour were strongly influenced by inter-male separation distance; these included: (1) the rate of display production; (2) number of displays (volley length); (3) types of displays performed; and (4) displays with dewlap extension. The rate of displaying increased with decreasing inter-male separation distance, being 1.4 ± 0.28 , 2.0 ± 0.33 and 3.8 ± 0.35 displays/min at separation distances greater than 100 cm, within 20–100 cm and less than 20 cm, respectively.

Solitary displaying tended to increase with decreasing inter-male separation distance. Of solitary displays, 5% occurred at separation distances greater than 60 cm; most (83%) were performed when males were within 20 cm of one another. Conversely, volley length tended to decrease with decreasing inter-male separation distances; 81% of volleys performed at longer inter-male distances (> 60 cm) contained three or more displays, while short volleys (two displays/volley) predominated (53%) at shorter inter-male distances (< 60 cm).

Display type usage appeared to covary with both volley length and inter-male separation distance. The type C display predominated at separation distances greater than 20 cm (Fig. 6). Similarly, the type C display dominated long volleys (\geq four

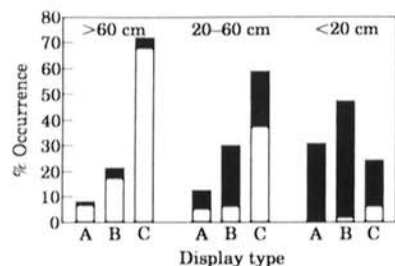


Figure 6. Proportion of three display types performed at three separation distances in the male-male context with (□) and without (■) dewlap extension performed by 34 male *A. carolinensis*, based on 453 type A, 756 type B, and 773 type C displays.

displays/volley) which were comprised of 2, 19 and 79% type A, B and C displays, respectively. Type B displays became the most frequent display at short separation distances (< 20 cm) (Fig. 6) and in short volleys (\leq three displays), which were comprised of 10, 46 and 41%, type A, B and C displays, respectively. The difference in display composition between short and long volleys was significant ($\chi^2 = 29.9$, $df = 2$, $P < 0.001$).

The male-male displays frequently lacked dewlap extension (Fig. 5), with dewlap use dramatically decreasing with decreasing separation distance (Fig. 6). At separation distances greater than 60 cm, dewlap extension accompanied 92% of the displays, but appeared with only 7% of the displays performed within 20 cm of an adversary.

Total number of bobs in the S3 sections of the displays increased as males shifted from advertisement to combat situations. Both type A and B displays had a significantly greater number of S3 bobs in the male-alone context than in the male-male context (Wilcoxon rank-sum test, $df = 2$; type A display, $\chi^2 = 4.7$, $P < 0.03$; type B display, $\chi^2 = 8.82$, $P < 0.003$). Type C displays also had this directionality, although the difference in mean bob number was not significant (Wilcoxon rank-sum test, $\chi^2 = 1.45$, $df = 2$, ns). In male-male encounters, the mean number of headbobs in S3 also decreased significantly with decreasing separation distance ($\bar{X} \pm SE = 3.6 \pm 0.24$, 3.3 ± 0.21 and 2.7 ± 0.15 , at separation distances greater than 60 cm within 20-60 cm and less than 20 cm, respectively) (Kruskal Wallis test, $\chi^2 = 9.47$, $df = 2$, $P < 0.009$).

Additional presentations of the data set can be found elsewhere (DeCourcy 1991).

DISCUSSION

Comparison with *Anolis*

The territorial display behaviour of male *A. carolinensis* demonstrated similarities with, as well as marked differences from, the generalized *Anolis* profile. Male *A. carolinensis* are similar to a number of other anoles in having a multiple display repertoire of stereotyped headbob patterns (e.g. Stamps & Barlow 1973; Hover & Jenssen 1976; Jenssen & Rothblum 1977; Jenssen & Gladson 1984). Male *A. carolinensis* have at least three distinct, stereotyped headbob patterns (A, B and C).

An unusual feature common to all three *A. carolinensis* displays is the way in which the dewlap is used. As expected, dewlap extension was stereotyped, being predictably timed with specific headbobs in the S2 section of all three display types; however, the finding that the dewlap could be withheld during the performance of any of the three display types was unexpected. Thus, for each display type there were two variants, one with and one without dewlap extension. Because dewlap extension occurred at a predictable point in the stereotyped bob pattern, we did not consider the dewlap component as an optional, independent behaviour in the sense of a display modifier (Jenssen 1979); if dewlap extension were independent, the displayer would be expected to demonstrate much more flexibility over when and how the dewlap was extended during a display. On the other hand, because the dewlap extension occurred at the same point and manner in all three headbob patterns, it did not contribute to any uniqueness between the display types. Thus, we were conservative in interpreting the number of display types in the *A. carolinensis* display repertoire. There seems to be three (rather than six) display types, each with its two variants of dewlap-present and dewlap-absent.

Male-alone displaying is performed in an 'assertion' context, the social context in which males perform non-directed displays with no particular individual targeted as a recipient; this context functionally identifies advertisement signals. Almost all (97%) of the *A. carolinensis* male-alone displaying occurred with dewlap extension. If the advertisement function of the displays in the male-alone context is to have the greatest impact, the signals require high visibility (Fleishman 1988a, b). Certainly the pink dewlap contrasting against the

habitat would significantly amplify the conspicuousness of the headbob signal. An unexpected feature of solitary *A. carolinensis* males involved the choice of display type; all three display types were used. This is in contrast to other anoles having more than one display type, where a single display type is reserved for the assertion context (Stamps & Barlow 1973; Jenssen 1977).

Male-male displaying is performed in the 'challenge' context, a social context in which displays are directed at a rival conspecific in a contest of intimidation. For challenging *A. carolinensis* males, the three display types and their dewlap variants used in the assertion context were the same physical displays used in the male-male interactions; the manner in which the displays were employed, however, differed between the social contexts. The dewlap was frequently withheld in the challenge context. Displays with dewlap extension became progressively less frequent as males approached each other. When males were less than three body lengths apart (< 20 cm), only 7% of displays exhibited dewlap extension. Because male *A. carolinensis* aggression frequently culminates in prolonged jaw locking (Greenberg & Noble 1944), an extended dewlap within lunging distance of an opponent could be grabbed and injured. In similar fashion, disputing male *A. limifrons* switch to a headbob-only display at short separation distances (Hover & Jenssen 1976).

Display rate, volley length and display type also covaried with male separation distance. At large separation distances, long volleys of displays were common, solitary displays rare, and type C displays predominated. As the males moved closer together, more type A and type B displays were used. The display rate in the challenge context rose eight-fold over that of the advertisement context, and as males closed from 100 cm apart to within 20 cm, the display rate rose an additional two-fold.

Carolinensis Displays: Previous Descriptions Compared

McCardell (1971) filmed 187 displays by nine males in his study of temperature effects on display duration. Individual components (units) within headbob displays and the criteria for differentiating between display types were not discriminated because total display duration was the variable of interest. McCardell presented one DAP-graph that resembled our type C display.

Crews (1975) performed a quantitative analysis of displays by male *A. carolinensis*, relying primarily on event recorder data. Dewlap extension was the reference point for counting the bobs occurring before and during dewlap extension. No mention was made of how displays were handled if and when dewlap extensions were absent. Crews followed Carpenter's (1962) functional terms, reporting that male *A. carolinensis* have four displays, three with dewlap extension (challenge, assertion and courtship displays) and one with only head bobbing (submission display).

During male encounters, Crews found a single challenge display with much inter-male variability; we found three display types (A, B and C, each with and without dewlap extension) performed by all subjects, with no appreciable inter-male differences. Perhaps it was these three display types that contributed to the variability Crews reported. Where Crews listed an assertion display, we found the same three display types (A, B and C) to be the only display patterns performed during the advertisement or assertion context. There was no evidence for an assertion display specific to the assertion context. Because of the differences in data presentation, it was not possible to compare headbob displays that lacked dewlap extension (Crews' submission displays versus our type A, B and C variants without dewlap extension).

Sigmund (1978) based his study on a frame-by-frame analysis of 232 filmed displays by 15 male *A. carolinensis* pooled from various social contexts. Sigmund analysed his DAP-graphs by dividing the displays into three 'units' which roughly corresponded to our S1, S2 and S3 sections. His unit 1 contained one or two bobs (our S1 contained one to three bobs and defined the three display types), unit 2 contained a pair of bobs (as did our S2), and unit 3 contained one to five 'sub-bobs' (our S3 varied from one to nine bobs). If the dewlap appeared, it was extended at the beginning of unit 3. Sigmund's analysis and ours are very similar to this point. However, he recognized only a single display, even though his unit 1 contained evidence for at least two display patterns; two patterns are actually indicated in his presented DAP-graphs (figures 2 and 3 in Sigmund 1978). His analysis might have revealed more than one pattern if his units had been based on separate bobs and their intervening pauses.

The demes from which the subjects of the two studies were collected may contain phenotypic differences in display structure, contributing to some

of the deviation between our results (three display types) and Sigmund's data (no more than two headbob patterns). Using electrophoretic data, Wade et al. (1983) reported a marked genetic distance between *A. carolinensis* from Gainesville, Florida (near our collection site), and those from New Orleans, Louisiana (Sigmund's source).

Bels & Goosse (1987) used DAP-graphs to analyse 25 displays performed by five subjects in the male-male context. Like McCardell (1971), they presented a single headbob pattern for the territorial displays of male *A. carolinensis* that closely resembled our type C display. Bels & Goosse suggested, without descriptive statistics, that there was intra-population variability in the display.

Problem of Function-labelling

Functionally naming a behaviour has been a longstanding concern (Tinbergen 1951). Choosing a display label that reflects a perceived function or causation can create two basic problems. The first problem arises when other functions or causations for a display are uncovered. Now what is the behaviour to be called? A second problem arises if a functional label precedes an accurate descriptive analysis of the display performances, such that several labels may be assigned to the same display or several displays may go undifferentiated under the same label. Once understood, what are the various behaviour patterns to be called?

Descriptions of the visual signals of lizards (Carpenter 1986), including those of *A. carolinensis*, have been troubled by both of the above problems. There is a tendency to assign labels to displays on the basis of the social context in which the displays appear. This is in partial consequence of the nomenclature employed in early work on iguanid lizard display behaviour. Most notable are the terms, assertion display and challenge display (Carpenter 1962). Carpenter referred to a species' headbob pattern as an assertion display if a territorial male performed the display with no conspecifics nearby (assertion context), and as a challenge display if a display male aggressively engaged another male (challenge context). Carpenter observed only a single, species-specific display pattern (as shown by DAP-graphs) for each of his studied species; thus, males of a species were using the same headbob cadence (i.e. headbob signal) in both contexts. The distinction in the displays between the two contexts was the addition of

postural changes (display modifiers, Jenssen 1979) during aggressive interactions. The assertion-challenge notation was not intended to indicate two different kinds of displays. Carpenter pointed out (1978, page 11), 'assertion and challenge are considered as only difference in intensity of the display'.

The convenience and precedence of context-labelling have encouraged the assumption of a single physical signal for each social context (e.g. an assertion display, a challenge display and a courtship display) at the expense of not performing an adequate descriptive analysis on the observed species' signal repertoire. The consequence of such procedures obfuscates the reality of a species' communication system. The misconceptions could range from: (1) the same physical headbob pattern, used exclusively in all social contexts, being called by a variety of terms to (2) a complex of headbob patterns, employed in a particular context, being lumped as one display. In the end, functional labels discourage prerequisite descriptions of the physical structures of signals and the rules by which the respective signals are used within and between social contexts. Only after signal structure and its contextual use are known can function be inferred.

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