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Reviewed work(s):

Source: *Herpetologica*, Vol. 55, No. 2 (Jun., 1999), pp. 222-234

Published by: [Herpetologists' League](#)

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Accepted: 24 April 1998

Associate Editor: Allison Alberts

Herpetologica, 55(2), 1999, 222–234
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COMPARISONS OF TEMPORAL DISPLAY STRUCTURE ACROSS CONTEXTS AND POPULATIONS IN MALE *ANOLIS CAROLINENSIS*: SIGNAL STABILITY OR LABILITY?

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ABSTRACT: We examined the relative stability versus lability of temporal display structure in males of the lizard *Anolis carolinensis*. We videotaped headbobbing displays across field and laboratory environments, social contexts, and populations for males from Georgia, Florida, and Hawaii, and subsequently generated display-action-pattern (DAP) graphs of these displays for statistical comparison. *Anolis carolinensis* is known to be a recent (circa 1950) colonizer of Hawaii, and displays from this population could therefore be altered through founder effects, genetic drift, and/or a tropical environment unlike that encountered over the rest of the species' range. Therefore, we expected to find lability in temporal display structure between Hawaiian and mainland populations. In contrast, we found that males from each population used the same three, highly stereotyped temporal display structures (i.e., display types, labeled A, B, and C) in their display repertoires, and that all three of these types were used across all measured recording environments and social contexts. Furthermore, intra-display structure was not affected by recording environment or social context, but within the relatively small total variance, a significant population effect was found for a majority of intra-display units.

Key words: Sauria; *Anolis carolinensis*; Communication; Display; Intraspecific variation

COMMUNICATION signals, both their physical structure and their functional expression, are shaped by numerous and potentially antagonistic selection pressures resulting from features of the biotic and abiotic environments (e.g., Endler, 1992; Fleishman, 1992; Hailman, 1977; Ryan

and Rand, 1990). Yet, despite diverse selection pressures, communication signals frequently share some commonly recognized features. Structurally, these signals tend to be species-typical with pronounced stereotypy (Barlow, 1968) in both invertebrates (e.g., Bentley and Hoy, 1972; Lloyd, 1975) and vertebrates (e.g., Hauser, 1996; Jenssen, 1977, 1978; Marler and Peters, 1977; Ryan and Rand, 1993a,b; Tin-

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bergen, 1951). As a result, these species-typical signals can play an important role in evolution as reproductive isolating mechanisms (*sensu* Mayr, 1970) in the initiation of speciation and the maintenance of genetically distinct groups.

Given the ubiquitous need for communication to coordinate social activities, to what extent might signal structure be stable or labile? This question may be addressed at several levels. First, one could examine the degree of variation in a signal within and among individuals in a single population (e.g., DeCourcy and Jenssen, 1994; Jenssen, 1971; Martins, 1991, 1993a) to gain insight into the potential for signal structure to convey arousal level, individual identity, or context-specific information. Second, one could examine variation across populations of a single species (e.g., Carpenter and Ferguson, 1977; Ferguson, 1971; Ryan et al., 1992) to gain insight into the selective influence of environment on signal expression. Third, one could examine variation in a communication signal across closely related species (e.g., Kusmierski et al., 1997; Martins, 1993b), yielding insight into the evolutionary history of signal structure, and potentially into phylogenetic relationships among closely related species. In the present study, we examined the relative stability of the temporal structure of male headbobbing displays in *Anolis carolinensis* across field and laboratory environments, social contexts, and populations.

Anoline headbobbing displays (1) are species-specific body movements that raise and lower the head and/or dewlap, (2) are typically highly stereotyped (but see Jensen, 1979a), (3) are shared by the population, (4) have a strong genetic component, and (5) function in communication (Jenssen, 1977). Headbobbing displays can be conceptually divided into core and modifier components (Jenssen, 1977). The core component of anoline signals is the display type—a species-specific temporal headbobbing pattern that is predictably performed across all displays of the same type (Jenssen, 1977). Modifiers are postures (e.g., sagittal expansion, lateral presentation) or movements (e.g., introduc-

tory head bows, leg extension-flexion) which may be added to the core display, are not typically associated with any particular display type, and appear to be evolutionarily conservative, as many modifiers appear across lizard taxa (Jenssen, 1977). In general, core display structure can convey individual and species-level information, while display modifiers appear to augment core displays in a graded fashion to convey relative arousal of the displayer (e.g., Jenssen, 1977, 1979b; Martins, 1991, 1993a). In our study, we focus on potential variation in core display structure.

The headbobbing displays of *A. carolinensis* provide an opportunity to examine the extent of signal variance due to environmental and social contexts, individuals, and populations. This species is (1) known to display readily under field and laboratory conditions and in different social contexts (e.g., DeCourcy and Jenssen, 1994; Jenssen et al., 1995), (2) widely distributed in the southeastern United States (Conant, 1975) over areas of considerable variation in structural habitat, climate, and fauna, and (3) a recent colonizer (circa 1950) of Hawaii (McKeown, 1996) which is environmentally very different from mainland population locales. We used these species traits (1) to determine if males from three geographically disjunct populations of *A. carolinensis* possess the same display types within their repertoires, (2) to compare intra-display structure (in terms of temporal patterning) of adult males of *A. carolinensis* within populations across various contexts (e.g., natural and captive, conspecific and heterosexual interactions), and (3) if population display types are the same, then to compare intra-display structure among populations. Displays of Hawaiian *A. carolinensis* could reflect influences from founder effects, genetic drift, and/or a tropical environment unlike that encountered over the rest of the species' range. Therefore, we expected to find high population-level lability in the Hawaiian display repertoire, with mainland populations showing more similarity to each other than to the Hawaiian population.

MATERIALS AND METHODS

We studied the displays of 50 adult males (snout-vent length, SVL \geq 55 mm) of *A. carolinensis* from three populations in the United States: (1) 15 males from the "GA" population of Augusta, Georgia (latitude 33° N, \bar{x} annual temperature = 17.3 C, \bar{x} monthly precipitation = 8.4 cm), (2) 22 males from the "FL" population of Palatka, Florida (latitude 30° N, \bar{x} annual temperature = 20.3 C, \bar{x} monthly precipitation = 9.7 cm), reanalyzed from DeCourcy and Jenssen (1994), and (3) 13 males from the "HI" population of Hilo, Hawaii (latitude 20° N, \bar{x} annual temperature = 23.3 C, \bar{x} monthly precipitation = 23.2 cm) (Table 1).

We videotaped displays in the field or in the laboratory at Virginia Polytechnic Institute and State University. In the field, free-ranging, unmanipulated males were videotaped from a distance of \geq 3 m using a Panasonic video camera (AG 460) fitted with an Aztec video telephoto converter (2.0 \times) to increase subject magnification. In the laboratory, males were housed either alone or with a female in 0.6 \times 0.6 \times 0.7 m glass-fronted wooden enclosures, with a peat moss substrate and a simulated natural habitat of branches, stumps, and artificial vegetation. We fed all lizards crickets (*Acheta domesticus*) dusted with calcium lactate daily. Water was available in shallow dishes and through daily misting of the enclosures. Fluorescent (Philips F40CW, 40 W tubes) and incandescent (General Electric 150 W flood lights) lighting was used for each enclosure on a 14:10 h light:dark cycle, and cage temperatures ranged from 35 C directly under flood lights during the day to 24 C at night.

Free-ranging males videotaped in the field performed displays in the following three contexts. Male-alone displays (M-A) occurred when territorial males perched in prominent locations within their territories and signaled in a non-directed, advertisement manner (i.e., with no other lizards visible). Male-male (M-M) displays occurred whenever two males exchanged displays across territory boundaries, but were not accompanied by fighting because

TABLE 1.—Sample sizes of subjects and displays (in parentheses) of males of *Anolis carolinensis* by display type (A, B, C) within social contexts (male-alone = M-A, male-male = M-M, male-female = M-F), within recording environment (field or laboratory), and within population (Georgia = GA, Florida = FL, Hawaii = HI).

Popula- tion	Recording environment														
	Field						Laboratory								
	M-A, M-M*		M-F		M-A		M-M		M-F		M-A				
A	B	A	B	A	B	A	B	A	B	A	B	C			
GA	4(10)	4(16)	7(28)	7(13)	6(16)	9(59)	7(44)	9(70)	11(76)	12(52)	15(69)	16(73)	4(30)	5(29)	5(66)
FL															
HI	5(6)	5(10)	10(36)	2(3)	2(8)	9(49)									

*M-A and M-M field contexts were pooled due to small M-M sample sizes.

territories were established prior to the onset of videotaping. Male–female (M–F) displays occurred whenever a resident male and female were interacting.

For displays recorded in the laboratory, we simulated the three field contexts described above as follows. For the M–A and M–M contexts, a single male was placed into each of two observation enclosures (constructed and furnished identically to the housing enclosures) positioned end-to-end and divided by a removable central partition. Males were given 4–7 days to acclimate to the enclosure before recording M–A displays of each male for 30 min. Immediately thereafter, the partition was removed to allow previously isolated males to come into contact, thus creating the M–M context. During the resulting agonistic encounter, which often included fighting, the displays of both males were videotaped for up to 75 min, or until one male fled from the encounter. For male displays recorded during the M–F context, a male and female pair was allowed seven days to acclimate together within an observation enclosure, then their behavior was videotaped for 30 min. Immediately thereafter, a new female was placed into the cage to stimulate further courtship, and the subsequent interaction was videotaped for an additional 60 min. Displays unequivocally directed towards females were then chosen for analysis. Videotaping in the laboratory was performed using two Panasonic television cameras (WV 1500), outfitted with 16–160 mm zoom lenses, to obtain large images while simultaneously recording both subjects with a split-screen generator (Vicon V270SP) and a Panasonic VCR (AG 1950).

We analyzed videotaped displays frame-by-frame using the Display-Action-Pattern (DAP) graph method (e.g., Carpenter and Grubitz, 1961; Jenssen, 1978) which plots the vertical amplitude of the lizard's head and dewlap (y-axis) over elapsed time (x-axis) for each display. DAP-graphed displays were divided into naturally occurring sequential units that consist of headbobs and inter-bob pauses (odd- and even-numbered units, respectively; Fig. 1). The duration of sequential units defined the ca-

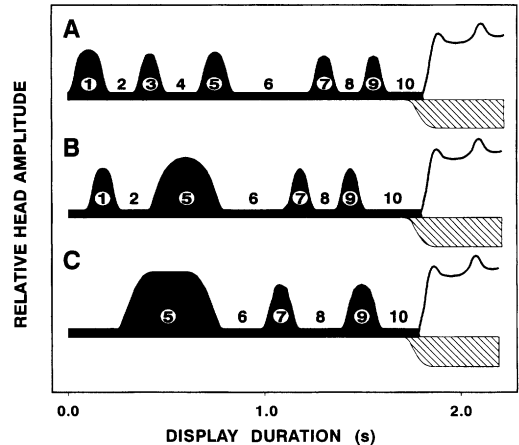


FIG. 1.—Generalized Display Action Pattern (DAP) graphs of A, B, and C display types for adult males of *Anolis carolinensis* from Georgia, Florida, and Hawaii. Display units (numerals 1–10) are numbered following the convention established by DeCourcy and Jenssen (1994). Head amplitude is plotted above the x-axis relative to elapsed time, with stereotyped display types shown in solid black and terminal, variably produced headbobs shown by a black line. Dewlap extension is plotted below the x-axis, and may be present or absent for each display type. Display unit durations are overall mean values combined from all study populations. Modified from DeCourcy and Jenssen (1994).

dence pattern of a display, and displays of a common cadence were categorized as being of the same display type. DAP-graphed displays were classified according to population, context, subject, and type, and unit durations, with the latter quantified to the nearest 0.033 s (the resolution of our VCR).

Our protocol was contingent on the outcome of our first objective (see Introduction) because it affected our approach to the subsequent two objectives. In this regard, all three populations of *A. carolinensis* performed the same three recognizable A, B, and C display types (Fig. 1). To confirm the accuracy of visual display type classification, we used a nearest neighbor discriminant analysis to separate displays into categories based on display units 1–10. For GA and HI, the discriminant analysis agreed with 100% of our initial placements (267/267 and 112/112 displays, respectively), and for FL it agreed with 99.5% (382/384 displays). Because the

presence or absence of certain combinations of units 1–4 are diagnostic for the A, B, and C display types (Fig. 1), it was not surprising that there was excellent discrimination of the display types. However, even when limiting the nearest neighbor discriminant analysis to units 5–10 (the units common to all display types), there was still excellent agreement with our visual typings (GA 96%, FL 92%, and HI 100%). Therefore, we followed DeCourcy and Jenssen (1994) in labeling the DAP-graphed displays as A, B, or C display types and in the numbering of display units within each display type (Fig. 1).

We performed all statistical comparisons of intra-display structure (i.e., comparisons of display units among displays of the same type) using intra-subject means to eliminate sample bias resulting from unequal numbers of displays from different individuals. Descriptive statistics are reported as means (\bar{x}) \pm 1 SE, and hypothesis tests were two-tailed. All statistical analyses were performed with the statistical software program Minitab Release 10 Xtra (1995), and the level of significance required to reject the null hypothesis was $P \leq 0.05$.

RESULTS

Intra-population Effects

The intra-display structure of A, B, and C display types was virtually unaffected by whether the recording environment was in the field using free-ranging males under natural conditions, or in the laboratory using captive males. We used Kruskal-Wallis tests ($df = 1$) to compare the individual unit durations within each display type across contexts. We first examined display structure for stability in the laboratory by comparing between the M–F field and the M–F laboratory contexts for the GA population (for sample sizes, see Table 1). This comparison held context and population constant so that only the recording environment differed. Only two out of the possible 24 total display units for the three display types (Fig. 1) were found to be significantly different in duration (U5 of type B, $H_1 = 4.05$, $P = 0.044$; U7 of type C, H_1

$= 6.93$, $P = 0.009$). Because of the small number of unit differences, we pooled the M–F laboratory and field data in subsequent comparisons.

Next, we examined whether any of the three display types are restricted to certain social contexts (i.e., M–A, M–M, M–F) or whether unit durations of common display types might be altered if a display type is used across these contexts. As with recording environment, all three display types were used across contexts (i.e., there were no context-specific display types), and context affected display structure minimally. Comparisons using Kruskal-Wallis tests ($df = 1$) between the M–A and M–M context displays performed in the laboratory by the FL males revealed that only one of the 24 units compared for the three display types was significantly different (U1 of type B, $H_1 = 4.61$, $P = 0.032$). Therefore, because displays do not appear to differ between the M–A and M–M contexts, and due to the infrequent M–M displays from field subjects, displays from the M–A and M–M contexts were pooled in subsequent analyses. Comparisons between the M–A/M–M and M–F display units within each of the A, B, and C display types in the GA population revealed that none of the 24 units were significantly different (all values of $P > 0.061$). Comparisons of the M–A/M–M and M–F displays for the HI population also indicated there were no significant differences in the six units compared for type C displays. A small sample size precluded an analysis for A and B display types for HI (Table 1).

Inter-population Effects

As neither recording environment nor social context particularly affected display type structure, displays of the same type and population were pooled from all contexts to compare mean unit durations among populations (Table 2). Kruskal-Wallis tests on total display duration for each display type found no significant differences among populations in total display duration (i.e., the sum of all unit durations in a display: Table 2). However, there was some variation in how total display duration was divided into unit durations among

TABLE 2.—Descriptive statistics and Kruskal–Wallis tests ($df = 2$) for individual unit durations of display types A, B, and C comparing among Georgia (GA), Florida (FL), and Hawaii (HI) populations of males of *Anolis carolinensis*. Within each population and display type, means of intra-subject means are shown, and sample sizes are given in parentheses for GA, FL, and HI, respectively. Units marked with different superscripts are significantly different from each other and from unmarked units in the same row.

Display (n)	Unit	GA		FL		HI		H_2	P	
		\bar{x} (s)	SE	\bar{x} (s)	SE	\bar{x} (s)	SE			
Type A (12,17,7)	U1	0.201	0.005	0.192	0.017	0.212	0.015	3.73	0.155	
	U2	0.082	0.008	0.174 ^a	0.025	0.102	0.011	13.32	0.001	
	U3	0.133	0.004	0.119	0.006	0.176 ^a	0.021	11.51	0.003	
	U4	0.150	0.011	0.158	0.013	0.126	0.031	3.22	0.201	
	U5	0.153	0.011	0.142	0.011	0.174	0.018	3.17	0.205	
	U6	0.382	0.018	0.320	0.013	0.317	0.047	5.94	0.052	
	U7	0.134 ^a	0.005	0.104 ^b	0.005	0.171	0.013	20.59	<0.001	
	U8	0.073 ^a	0.004	0.138 ^b	0.008	0.105	0.016	19.01	<0.001	
	U9	0.116	0.004	0.105	0.004	0.148 ^a	0.010	10.80	0.005	
	U10	0.154	0.012	0.238 ^a	0.014	0.129	0.020	17.26	<0.001	
	U1–10	1.58	0.028	1.69	0.050	1.66	0.043	3.92	0.142	
Type B (11,21,6)	U1	0.154	0.004	0.152	0.012	0.177	0.010	5.53	0.064	
	U2	0.142	0.007	0.170	0.021	0.106 ^a	0.006	7.54	0.023	
	U5	0.369 ^a	0.010	0.324	0.012	0.335	0.021	7.34	0.026	
	U6	0.296	0.016	0.221 ^a	0.014	0.306	0.027	12.87	0.002	
	U7	0.130	0.005	0.125	0.009	0.185 ^a	0.015	11.22	0.004	
	U8	0.074	0.006	0.128 ^a	0.012	0.081	0.014	11.63	0.003	
	U9	0.133	0.004	0.130	0.008	0.169 ^a	0.012	9.41	0.011	
	U10	0.240 ^a	0.013	0.317 ^b	0.019	0.171	0.012	17.27	<0.001	
		U1–10	1.54	0.031	1.57	0.025	1.53	0.033	0.40	0.818
	Type C (15,22,13)	U5	0.492	0.012	0.437 ^a	0.015	0.516	0.011	13.52	0.001
U6		0.202	0.019	0.188	0.019	0.198	0.008	1.93	0.381	
U7		0.134	0.005	0.134	0.008	0.182 ^a	0.006	16.34	<0.001	
U8		0.190	0.006	0.247 ^a	0.010	0.198	0.007	17.01	<0.001	
U9		0.172	0.004	0.173	0.010	0.209 ^a	0.008	9.23	0.010	
U10		0.172	0.009	0.221 ^a	0.011	0.150	0.007	18.95	<0.001	
	U1–10	1.36	0.031	1.40	0.029	1.45	0.023	5.08	0.079	

populations. We found that six of 10 type A units, seven of eight type B units, and five of six type C units showed significant inter-population differences, and rank-based pairwise multiple comparisons (Hollander and Wolfe, 1973) identified the unit differences among the three populations (Table 2). Furthermore, nearest neighbor discriminant analyses for each display type correctly identified population for 87% of type A, 91% of type B, and 66% of type C displays. Thus, some lability within display type structure exists at the inter-population level of comparison, whether examined by their constituent units (Kruskal-Wallis tests) or as whole entities (nearest neighbor discriminant analyses).

We also compared the relative stereotypy of display types A, B, and C among GA, FL, and HI samples as a potential reflection of stabilizing selection. To do this, we calculated the coefficient of variation

(CV) of individual mean unit durations for each display type (Table 3). By convention, behavioral units that have CV's $\leq 35\%$ are considered highly stereotyped (Barlow, 1968). All 24 GA units, 18/24 FL units, and 19/24 HI units were highly stereotyped. Additionally, overall display type CV's (calculated as the mean of unit CV's within a display type) ranged from 13.1–33.4% (Table 3), thus indicating high stereotypy for each display type in each population. Nevertheless, Kruskal-Wallis tests indicated an overall significant difference in display type CV's among populations for each display type. Rank-based pairwise multiple comparisons indicated that for type A, GA had a significantly lower median CV than HI; for type B, GA had a significantly lower median CV than FL; and for type C, HI had a significantly lower median CV than FL (Table 3). Thus, no population had a consistently higher or

TABLE 3.—Mean display unit coefficients of variation (CV's) and overall mean CV's for type A, B, and C displays among Georgia (GA), Florida (FL), and Hawaii (HI) populations of males of *Anolis carolinensis*. Individual unit CV's were calculated using means of intra-subject means. Display type CV's are means of individual unit CV's within each display type. CV's marked with different superscripts are significantly different from each other, based on Kruskal-Wallis tests ($df = 2$).

Display	Unit	Individual unit CV's (%)			Display type CV's (%)			H_2	P			
		GA	FL	HI	GA	FL	HI					
Type A	U1	7.9	37.3	18.3	19.3 ^a	28.4 ^{a,b}	32.5 ^b	6.65	0.036			
	U2	31.0	59.2	25.9								
	U3	12.1	21.5	32.6								
	U4	26.4	33.3	64.4								
	U5	25.4	31.5	26.1								
	U6	15.9	17.0	38.7								
	U7	14.5	18.6	20.6								
	U8	18.5	23.0	39.7								
	U9	12.9	17.2	18.9								
	U10	27.9	25.0	40.0								
Type B	U1	9.6	36.5	14.2	15.3 ^a	33.4 ^b	20.2 ^{a,b}	10.74	0.005			
	U2	16.0	55.9	13.1								
	U5	9.7	16.3	15.0								
	U6	18.1	28.1	21.0								
	U7	14.2	31.8	20.2								
	U8	26.0	43.6	43.3								
	U9	10.7	27.5	16.9								
	U10	17.8	27.6	17.6								
	Type C	U5	9.3	16.3	7.7	16.8 ^{a,b}	27.2 ^a			13.1 ^b	7.61	0.023
		U6	35.0	46.5	14.6							
U7		15.0	29.1	12.4								
U8		11.7	19.8	12.1								
U9		10.1	27.2	14.1								
U10		19.7	23.9	17.8								

lower stereotypy for its A, B, and C display types than any other population.

Given that GA, FL, and HI lizards are using the same display type repertoire, but that some variation exists in intra-display structure, we used a nested ANOVA with all 763 displays to determine the relative contribution of population, context, among-individual, and within-individual differences in display units to the total display variance (Fig. 2). Because the data were unbalanced, F -tests and P -values were not computed. We found that, on average, population accounted for 26% of the total variance in type A displays, 13% in type B displays, and 14% in type C. Context accounted for 5% of the variance in type A displays, 17% in type B, and <1% in type C. In contrast, among-subject differences were high, accounting for 36%, 34%, and 42% of variance in type A, B, and C displays, respectively. The remainder of the variance (33%, 36%, and 44%)

was residual, and included within-subject and measurement error components. Thus, for highly stereotyped displays, among- and within-individual differences accounted for more of the existing variance than was due to inter-population differences.

Finally, we performed a cluster analysis to produce a graphical presentation of the structural relationship among the display types of GA, FL, and HI males of *A. carolinensis* (Fig. 3). Mean unit durations for each display type in each population were entered into the cluster analysis (i.e., $n = 9$; three display types, from each of three populations). To produce a dendrogram (Fig. 3), clusters were created using an average linkage algorithm, and similarity was measured using squared Euclidian distance (Hair et al., 1987); however, the relationships produced remained consistent regardless of the algorithm and distance measure used. As expected, inter-display

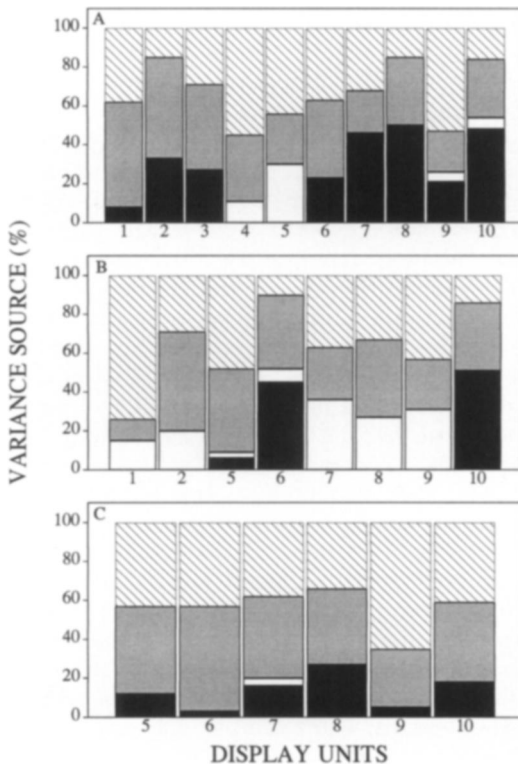


FIG. 2.—Proportion of variance in (A) display type A ($n = 158$), (B) display type B ($n = 218$), and (C) display type C ($n = 387$) unit durations attributed to population (black), context (white), among-individual (gray), and within-individual (hatched) components of a nested ANOVA on displays of adult male *Anolis carolinensis*.

type comparisons showed comparatively low similarity, and intra-display type comparisons across populations showed comparatively high similarity. Of particular interest, within each display type GA and HI displays were more similar to each other than either was to FL displays.

DISCUSSION

Intra-population Effects

We addressed whether (1) the temporal structure of a display type may be influenced by unnatural surroundings (e.g., laboratory enclosures), (2) display types or variation within display types may be context-specific, and (3) display types or variation within display types may be individual-specific. Our data supported none of these possibilities. When comparing the

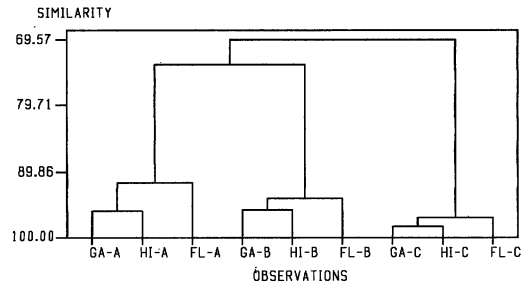


FIG. 3.—Dendrogram resulting from a cluster analysis on mean unit durations of display types A, B, and C from Georgia (GA-A, GA-B, GA-C), Florida (FL-A, FL-B, FL-C), and Hawaii (HI-A, HI-B, HI-C) populations of adult males of *Anolis carolinensis*. Clusters were created using an average linkage algorithm, and similarity was measured by squared Euclidian distance.

displays between free-ranging and captive lizards, there was virtually no laboratory effect on the temporal display structure for any display type, a conclusion made for other anoles as well (e.g., *A. nebulosus*: Jenssen, 1971; the *A. brevirostris* complex: Jenssen and Gladson, 1984). This lack of a laboratory effect, coupled with the fact that *Anolis* readily displays in the laboratory, should allow investigators to identify the temporal structures of display types using laboratory-held subjects. However, unlike display structure, other features of the display relevant to communication such as display rates may differ considerably between the field and laboratory (e.g., Jenssen et al., 1995).

There was no context-specificity for the stereotyped *A. carolinensis* headbobbing displays. The three display types (A, B, and C) were performed in each of the three basic social contexts of M-A (i.e., assertion context), M-M (i.e., challenge context), and M-F (i.e., courtship context). The absence of context-specific display types is not unusual for those species of *Anolis* that have only one stereotyped headbob structure (e.g., *A. nebulosus*: Jenssen, 1971; *A. cybotes*: Jenssen, 1983), because the single display type is used in all social contexts. However, for anoles that are known to have repertoires of multiple, stereotyped display types (e.g., *A. limifrons*: Hover and Jenssen, 1976; the *A. brevirostris* complex: Jenssen and Gladson, 1984; *A. aeneus*:

Stamps and Barlow, 1973), one display type is reserved for the assertion context, while the entire repertoire of display types is performed in both the challenge and courtship contexts. Therefore, *A. carolinensis* makes a departure from the norm by not having a display type exclusively used in the assertion context.

Because males use the same three display types in all of their social contexts, *A. carolinensis* is an excellent example of why the practice of categorizing displays by functional labels can be misleading. Using a convention originating with Carpenter (1962), albeit unintentionally (DeCourcy and Jenssen, 1994), investigators have often labeled the displaying activity during a particular social context with the functional label of that context. By this terminology, a lizard species will have an "assertion display", a "challenge" display, and a "courtship" display. However, it is obvious from our data that attempting to associate a specific and exclusive function to each of the A, B, and C display types would be spurious. If we had originally used the assumptions behind the functional convention, we would have overlooked the complexities and uniqueness of the communication system of *A. carolinensis*. Functional terminology, if applied before a quantitative description of headbobbing structure has been performed, can confound further understanding of display behavior. This has been a longstanding concern for all behavior patterns (e.g., DeCourcy and Jenssen, 1994; Greenberg, 1977; Martin and Bateson, 1993; Tinbergen, 1951), especially when investigators are interested in the description, function, and evolution of species-specific signals.

The temporal structures of the A, B, and C display types of *A. carolinensis* did not vary among the contexts that we measured, nor could we detect any individual-specific differences in the basic temporal headbobbing patterns of the A, B, and C displays. The latter conclusion directly contradicts that of Crews (1975), who reported significant inter-individual variations in displays of *A. carolinensis*. As reviewed by DeCourcy and Jenssen (1994), fundamental procedural differences most

likely produced the divergent results. Nevertheless, our data were not without some intra- and inter-individual variance in unit durations. The proportion of within- and among-individual variance in display structure was each as great or greater than that attributed to either context or population. This would suggest that the within-individual variance may convey displayer arousal level, while the among-individual variance may facilitate individual recognition. However, the total variance of the three highly stereotyped display types comes from display units that have an overall mean duration of 0.187 s, and an overall mean CV of 23.5% (computed from values given in Tables 2, 3, respectively). It is not apparent that the within- and among-individual differences in temporal display structure have been exaggerated (i.e., selected) to function as graded signals or as individual-specific markers. Should such functions exist in the signaling behavior of *A. carolinensis*, they are more likely conveyed by other means. For example, DeCourcy and Jenssen (1994) found that with changes in social context and inter-individual signaling distances, *A. carolinensis* will vary the use of dewlap during headbob displays, the display rate, the rapid sequences of displays (i.e., display volleys), and the proportions of A, B, and C display types. In addition, the non-stereotyped posturing and movements that optionally attend lizard headbobbing displays (i.e., display modifiers) appear in a graded and hierarchical manner to accentuate apparent body size and aggressive intent of the displayer during agonistic encounters (e.g., Jenssen, 1979b; Martins, 1993a; Ortiz and Jenssen, 1982). Finally, there are some species in which individual identity may be conveyed through headbobbing display characteristics alone (e.g., Greenberg and Jenssen, 1982; Jenssen, 1971, 1983) or through unique and repeatable combinations of headbobbing displays and associated modifiers (e.g., Martins, 1991).

Inter-population Effects

We addressed whether (1) overall display type pattern or variation within display types may be population-specific and

(2) colonization of atypical habitat may accentuate population-specificity or increased lability of display types. Some of these possibilities were supported, but not all. No display type was unique to any population; all individuals of *A. carolinensis* from all three populations performed the same three highly stereotyped A, B, and C display types. However, it is clear that the GA, FL, and HI populations have statistically distinguishable versions of these display types. Although the total duration of each display type did not differ among populations, a majority of intra-display unit durations showed significant inter-population differences, and nearest neighbor discriminant analyses were generally able to assign displays to the appropriate population. Furthermore, the FL display patterns showed a trend towards shorter headbob durations (10 out of 12 headbobs are shortest for FL: Table 2), and this trend was significantly different from what one would expect by chance alone (Chi-squared test; $\chi^2 = 15.25$, $P < 0.002$). Likewise, because there was no inter-population difference in overall display duration, FL inter-bob pauses were correspondingly longer in most cases when compared with GA or HI inter-bob pauses. Finally, FL display types B and C had the highest CV values. These results may suggest that GA, FL, and HI displays are diverging as a result of some type of selective pressure, but we are hesitant to draw conclusions on unit duration differences which were close to the limits of our analytical resolution.

In contrast to our expectation, the display type repertoire of HI *A. carolinensis* was not only identical to those of mainland populations, but the HI display types were more similar in structure to those of GA than GA was to FL (Fig. 3). Such a consistent finding across display types might indicate that HI *A. carolinensis* originated from GA-like stock or, less likely, that the selection pressures acting on the GA and HI displays are more similar than those affecting FL displays.

Overview

Our analyses have been restricted to the species-specific aspects of *A. carolinensis*

display behavior, specifically the stereotypical headbobbing patterns that we have called display types. The signal design of these conspicuous headbobbing displays should be sensitive to the constraints from local habitat features and predator pressure. Considering that *A. carolinensis* is broadly distributed over a variety of arboreal habitats, one would reasonably predict considerable inter-population variation in the species' display structure. However, what we found was somewhat unexpected in two ways.

First, the temporal structures of the display types were very stable across distant populations and their respective environmental differences, even for the Hawaiian population with its potential for founder effects and genetic drift. The inter-population stability of display types of *A. carolinensis* suggests that any small subset of a population colonizing available habitat would be representative of the species. Nevertheless, the 50 yr that *A. carolinensis* has been in the unique Hawaiian habitat would seem sufficient to produce some notable change in the displays of *A. carolinensis*. Baker (1996) found structural differences in the songs of singing honeyeaters (*Meliphaga virescens*) between island and mainland populations after approximately 75 yr of separation. Furthermore, Baker (1994) found these differences in song structure to have functional significance by reducing conspecific recognition across populations. Endler (1980) and Reznick and Endler (1982) found that guppy (*Poecilia reticulata*) coloration, important in male courtship displays, will evolve in 2 yr (10–15 generations) in response to changes in predation pressure. When predation on adults was decreased, male coloration intensified, and courtship display rates are known to be higher in male guppies with more conspicuous coloration (Luyten and Liley, 1991). Perhaps 50 yr is not sufficient time for behavioral divergence in *Anolis*. However, body and limb morphology of *Anolis sagrei* shifted in <15 yr to match habitat characteristics when it was experimentally introduced to several small islands in the Bahamas (Losos et al., 1997). Therefore, behavioral di-

vergence in 50 yr does not seem out of the realm of possibility given divergent selection pressures. Overall, behaviorally related traits, particularly those functioning in reproduction, are commonly considered to be evolutionarily labile. However, this expectation was not supported by our data for *A. carolinensis*.

Second, the communication potential of the three display types seems limited. The minimal variance in the temporal structure of each display type, for within- and among-individuals and across social contexts, negates a potential source of information (e.g., arousal, intent, individual recognition). Furthermore, because all three display types were used in all social contexts, there could be no differential functions ascribed among the display types, based on temporal structure alone. Given the structural stability of the A, B, and C display types across all examined conditions, we would conclude that these display types are under consistent stabilizing selection. However, the nature of that selection pressure is not clear. Most logically, intense selection for species-specific displays would suggest a species recognition function as a behavioral isolating mechanism. However, *A. carolinensis* historically has no sympatric congeners.

Further hypotheses may be generated as display types of *A. carolinensis* are observed from new perspectives. For instance, what might be the display structure and use by a small population of *A. carolinensis* in Florida whose communication signal includes a gray rather than pink dewlap (Michaud and Echternacht, 1995)? What is unique about the selective milieu of the gray-throated population, when all other populations across the southeastern United States are consistently pink-throated? In another approach, the degree to which the display patterns of *A. carolinensis* are phylogenetically conserved could be ascertained by examining the repertoire of display types of the closely related *Anolis porcatius*. *Anolis carolinensis* and *A. porcatius* were differentiated on the basis of allopatry alone (Buth et al., 1980; Williams, 1976). This question of the degree of similarity versus species-specificity is

particularly relevant now that *A. porcatius* is established in southern Florida and is, thus, sympatric with *A. carolinensis* (Mehaka et al., 1997). By continued investigation into the causations for display type stability of *A. carolinensis*, a larger picture for the function and evolution of lizard headbob display design may be revealed.

Acknowledgments.—We gratefully acknowledge J. Bradbury for her assistance with data analysis, and A. Alberts, R. Andrews, J. Bier, D. Duvernell, E. Martins, K. Passek, B. Wallace, and an anonymous referee for helpful comments on the manuscript. These data were gathered with the partial support of Financial Assistance Award Number DE-FC09-96SR18546 from the U.S. Department of Energy to The University of Georgia, a Virginia Polytechnic Institute and State University Biology Department Research Grant, and a Virginia Academy of Science Research Grant.

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Accepted: 20 February 1998

Associate Editor: Allison Alberts

Herpetologica, 55(2), 1999, 234–241
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RELATIONSHIP BETWEEN COPULATION DURATION AND SPERM TRANSFER IN THE LIZARD *ANOLIS SAGREI*

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ABSTRACT: I tested the hypothesis that copulation duration and the number of sperm transferred in a copulation are significantly correlated in the lizard *Anolis sagrei*. I also investigated whether copulation duration and number of sperm transferred in a copulation are affected by when in the breeding season a copulation occurs, by the body masses and snout-to-vent lengths (SVL) of the copulating lizards, and by which hemipenis is used in a copulation. Reproductively active males and females of *A. sagrei* were collected monthly in the Miami, Florida area from April through July of 1997 and housed in laboratory animal rooms. Two days after capture, males were allowed to copulate with sexually receptive females. I recorded copulation duration and whether the left or right hemipenis was used for each copulation. In addition, I estimated the number of sperm that were transferred to the female's cloaca in a copulation. Copulations by 46 different pairs of males and females were observed. Copulation duration varied significantly with the month of capture, but the estimated number of sperm transferred did not. Neither copulation duration nor estimated number of sperm transferred were significantly correlated with male or female body masses or SVL, or were significantly affected by which hemipenis was used. Copulation duration and the estimated number of sperm transferred in a copulation were not significantly correlated. Thus the hypothesis that copulation duration and sperm transfer are correlated in *A. sagrei* was not supported.

Key words: *Anolis sagrei*; Lizard; Copulation duration; Sperm transfer

In the lizard *Anolis sagrei*, males that are allowed to copulate under laboratory conditions vary significantly in copulation duration (Tokarz, 1988). Intraspecific variation in copulation duration may be widespread in lizards of the genus, *Anolis*, because males of *Anolis carolinensis*, a species not closely related to *A. sagrei* (Etheridge, 1959), have also been found to exhibit individually specific copulation durations (Crews, 1973, 1978).

Individual differences in copulation du-

ration among male anoles could be an important factor affecting male fitness for several reasons. First, there is indirect evidence that copulation duration may be positively related to the relative risk of predation in anoles, because the copulations of some species are relatively prolonged and often occur in exposed areas (Crews and Williams, 1977). Second, copulation duration could be a key factor influencing male reproductive success if the number of sperm that a male anole transfers in a