

Headbob Display Structure in the Naturalized *Anolis* Lizards of Bermuda: Sex, Context, and Population Effects

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ABSTRACT.—Many members of the Iguania group of lizards engage in stereotyped and species-specific “pushup” or “headbob” displays. Temporal attributes of displays have been quantified for a number of species in the genus *Anolis*, but few of these studies have examined effects on display structure of signaler sex, display context, and population. With this goal in mind we conducted a comparative study of three *Anolis* species permanently established (“naturalized”) on the island of Bermuda: *Anolis grahami* from Jamaica, *Anolis extremus* from Barbados, and *Anolis leachi* from Antigua and Barbuda. These anoles are distantly related to each other and to *Anolis carolinensis*—the only *Anolis* species for which all of the above influences on display structure have been examined in detail. Adults were field-captured and transported to the laboratory where paired interactions were videotaped and headbob displays analyzed. Results revealed one or more variables to exhibit sexual dimorphism in each species, and display context had little influence on signal structure. We then compared results from our founder populations on Bermuda with those published for two of our study species’ source populations. No significant differences in headbob display units were found between *A. grahami* on Bermuda and on Jamaica. In contrast, male *A. extremus* on Bermuda produced fewer units per display than did males from Barbados, although the nature of the published data prevented statistical comparison.

To be effective, animal signals must be both detectable against a background of irrelevant information and discriminable from other signals with which they might be confused (e.g., Guilford and Dawkins, 1991; Endler, 1992; Fleishman, 1992). By reducing within-signal variation or increasing between-signal variation, or both, selection tends to produce signals that are at once readily perceived and recognizable. Selection for signal stereotypy thus is anticipated to drive structural divergence of signal form within and among species, particularly for signals that facilitate mate recognition and reproductive isolation (e.g., Crews and Williams, 1977; Jensen and Gladson, 1984).

In the Iguania group of lizards, many taxa perform stereotyped and often species-specific “pushup” or “headbob” displays (e.g., Carpenter and Ferguson, 1977). These displays occur in multiple contexts, such as undirected signaling by territorial males, during courtship, in same-sex aggressive encounters, and in signaling to predators (e.g., Carpenter and Ferguson, 1977; Martins, 1991; Leal, 1999). Quantitative descriptions of headbob displays have been published for a number of species in the large genus *Anolis* (e.g., Jenssen, 1977a, 1979a,b, 1981, 1983; Scott, 1984; Bels, 1986; Fleishman, 1988; Font and Kra-

mer, 1989; Queral et al., 1995; Orrell and Jensen, 1998). Often absent from these studies, however, are comparisons of display structure between the sexes (Jenssen et al., 2000), among display contexts (DeCourcy and Jenssen, 1994; Lovern et al., 1999), and among populations of the same species (e.g., Jenssen, 1971, 1981; Lovern et al., 1999; Macedonia and Clark, 2001). Moreover, most studies that have examined potential sex, context, or population effects on *Anolis* display structure have been conducted on one species: *Anolis carolinensis*. Therefore, it is unknown how broadly the findings of these studies apply to the genus as a whole.

In the present study, we examine the potential effects of display variation attributable to sex of the signaler, display context, and population in three *Anolis* species permanently established (“naturalized”) on Bermuda: *Anolis grahami* from Jamaica, *Anolis extremus* from Barbados, and *Anolis leachi* from Antigua and Barbuda. These three species are neither closely related to one another nor to *A. carolinensis* (e.g., Jackman et al., 1999; Creer et al., 2001; Schneider et al., 2001).

The colonization of Bermuda by *A. grahami* has been well documented: 26 males and 45 females were deliberately introduced from Kingston, Jamaica in 1905 (Wingate, 1965; Losos, 1996). In contrast, the introductions of *A. extremus* and *A. leachi* appear to have been accidental, and both species are thought to have arrived roughly between 1940 and 1945 (Wingate, 1965).

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It is virtually certain that *A. extremus* and *A. leachi* became established on Bermuda from much smaller founder populations than *A. grahami*, and these differences seem to be reflected in their genetic variability. For example, in a study of 24 allozymes Gorman et al. (1976) found that Bermudian *A. grahami* retained about 82% of the heterozygosity of their source population, whereas in Bermudian *A. leachi* and *A. extremus* heterozygosity was approximately 56% and 16% that of their respective source populations. Given that performance of stereotyped headbob displays appears to be under relatively tight genetic control (e.g., Cooper, 1971; Stamps, 1978; Roggenbuck and Jenssen, 1986), one might anticipate differences in genetic variation between the source and founder populations of our study species to be borne out in their display structure.

In this work, we address four questions related to headbob displays in our study species. First, given the elaboration of male secondary sexual traits (e.g., dewlap) and strong sexual size dimorphism (SSD) in these anoles, we ask whether their headbob displays also exhibit sexual dimorphism. Specifically, we ask whether the sexes differ in the quantity of units produced per display by *A. grahami* and *A. extremus* (or the number of displays produced per volley by *A. leachi*, see below) and in the durations of displays and display units.

Second, although both sexes engage in headbob displays, males (1) use them during protracted ritualized contests with other males, (2) produce them far more frequently than do females and, unlike females, (3) broadcast them in a nondirected fashion in the course of daily activities (e.g., Jenssen et al., 2000). Because headbob displays appear to be under strong sexual selection in males, we ask whether display temporal structure reflects this selection differential by being more stereotyped in males than in females.

Third, we wish to know whether display structure is influenced by display context. Here, we ask whether temporal aspects of headbob displays differ between those performed in aggressive contests as opposed to those performed in courtship.

Last, given appreciable differences in genetic heterozygosity between the founder populations of our study species populations on Bermuda and their source populations in the Caribbean (Gorman et al., 1976, see below), we ask whether differences also occur between source and founder populations in display structure and stereotypy.

MATERIALS AND METHODS

Subjects and Housing.—Adult anoles were collected on Bermuda from 1–6 June and 22–27 No-

ember 1994 and transported to animal housing at Alma College (Alma, MI). Snout–vent lengths (mean \pm 1 SE, in mm) for subjects included in the present study were *A. grahami*, males (65.0 ± 0.6 , $N = 16$), females (46.0 ± 0.9 , $N = 6$); *A. extremus*, males (65.9 ± 1.9 , $N = 9$), females (52.0 ± 0.2 , $N = 4$); *A. leachi*, males (93.5 ± 2.1 , $N = 8$), females (68.3 ± 1.0 , $N = 8$).

Lizards were maintained in a room kept on a 14:10 L:D light cycle, 60–65% relative humidity, and temperature of 26–29°C. Ceiling- and wall-mounted full spectrum fluorescent lights provided ambient illumination. Individual lizards were housed in plastic cages (inside dimensions: 28 \times 17 \times 19 cm). Each cage included a perch (1.25-cm diameter wooden dowel) and 4-ply paper towel flooring that helped to maintain high relative humidity. Lizards were misted daily and alternately fed crickets and wax worms dusted with phosphorous-free calcium/D3 and reptile vitamins every three days.

Experimental Protocol.—Subjects were removed from their home cages and placed in wooden observation chambers (180 \times 39 \times 44 cm) fashioned after those illustrated in DeCourcy and Jenssen (1994) for 1–3 days prior to trials. Two full spectrum fluorescent bulbs and four 100-watt incandescent bulbs with aluminum reflector shields were suspended above each test tank to provide light and heat for basking on a 14:10 L:D cycle. A divider bisected each chamber so that the lizards on either side could not see each other until the divider was removed at trial commencement. Lizards in the observation chambers were misted with water twice daily and fed every other day. During the acclimation period for male-male trials (only), a conspecific female was placed in a small plastic cage near a basking block on each side of the observation chamber to potentiate male territorial behavior. These caged females were removed from the chamber several minutes prior to raising the center divider at the initiation of a trial.

Data Acquisition.—Lizard interactions were recorded using two camcorders mounted on tripods, with each camera following an assigned subject. A “screen-splitter” combined the two video images onto one tape with a time stamp. All lizard interactions were videotaped from behind a cloth blind, with small openings cut to accommodate the camcorder lenses.

Displays were quantified by superimposing a coordinate system over the video image of a displaying lizard (see Macedonia and Clark, 2001 for details). The changes in coordinates were compiled and display-action-pattern (DAP) graphs were produced (e.g., Carpenter, 1962; Jenssen, 1978).

To be consistent with previously published literature, displays were divided into odd- and

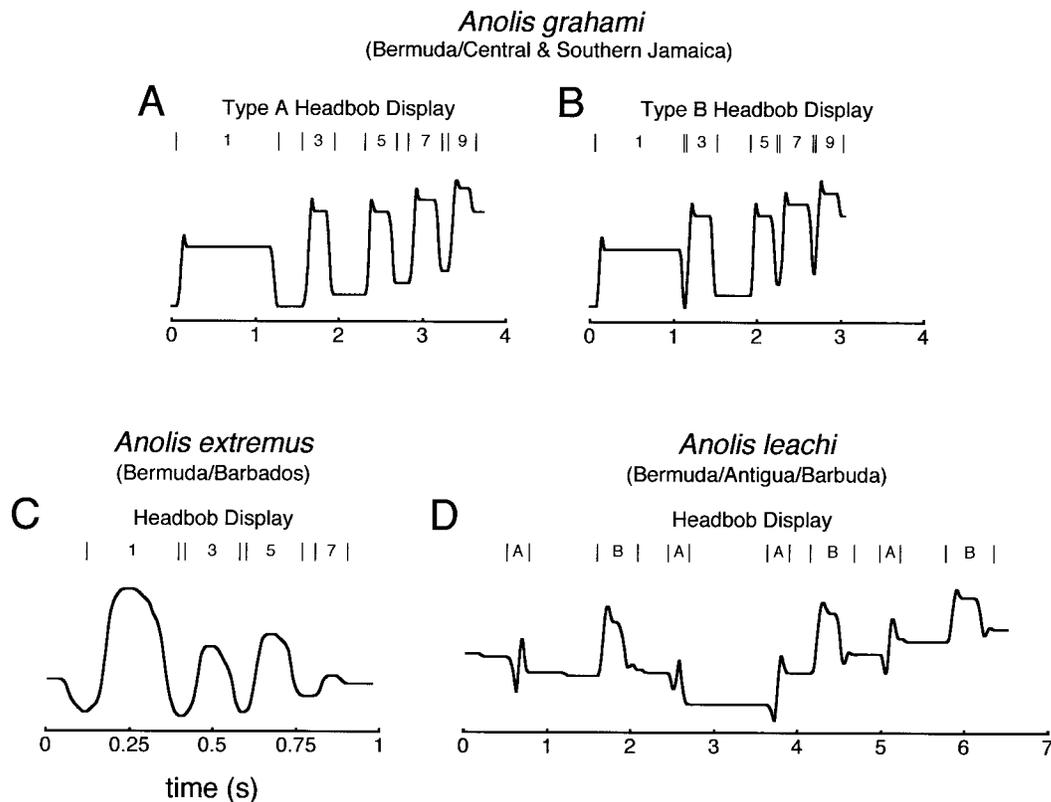


FIG. 1. Representative headbob displays from *Anolis grahami*, *Anolis extremus*, and *Anolis leachi* on Bermuda. (A) *A. grahami* Type A headbob display, (B) *A. grahami* Type B headbob display, (C) *A. extremus* headbob display, (D) *A. leachi* headbob display. Numbers in brackets above the displays indicate "odd numbered" display units; unlabeled "even numbered" units are pauses. In "d," letters in brackets indicate display type.

even-numbered units, where odd-numbered units define periods of motion and even-numbered units depict pauses. Unit lengths for each display were calculated as in Macedonia and Clark (2001).

Up to nine headbob units were measured for *A. grahami* displays to facilitate comparison with previously published work (Jenssen, 1981). Up to seven units were measured for *A. extremus* displays, as males rarely produced more than this. We arbitrarily required a minimum of seven display units for *A. grahami* (Fig. 1A–B) and five for *A. extremus* (Fig. 1C) for a display to be included in our quantitative analyses. By comparison, *A. leachi* produced "volleys" (Jenssen, 1977a) of displays, in which two display types were performed in a variable order (Fig. 1D). Because displays were brief (roughly the duration of one *A. grahami* display unit), we did not partition them into units.

Data Analysis.—We restricted our analyses to species-specific motion patterns termed "signature displays" (Jenssen, 1977a), although several other kinds of displays involving conspicuous

trunk/head motion were produced by our study species. Some examples included (1) long series' of nonstereotyped vertical head/trunk movements referred to as "step bobbing" (Rand, 1967; Jenssen, 1979b), (2) rapid, small amplitude vertical head movements variably termed "courtship bobs," "courtship-nods," "shudders," or "jiggles" (Carpenter and Ferguson, 1977; Jenssen, 1977a) and, in *A. extremus*, high amplitude "jerk bobs" (Stamps and Barlow, 1973). Unlike signature displays, these other motion patterns lack species specificity.

Potential effects of sex and context on temporal display structure were examined at the level of individual display units. Each subject contributed a single mean value for each display unit. We used the Mann-Whitney *U*-test to test for intraspecific sex differences in displays. The Wilcoxon Matched-Pairs Signed-Ranks test was used to test whether display unit durations differed between same-sex and opposite-sex contexts for male subjects that contributed displays to both contexts. We limited these latter analyses to males because females either did not ex-

TABLE 1. Headbob displays of *Anolis*: sample sizes by display context.

Context	Display	Number of displays (Mean \pm SE)	Total displays (N)
A. <i>Anolis grahami</i> adult males (N = 16) and females (N = 6)			
Male to male	Type A	5.6 \pm 1.5 (N = 90)	Males 209
Male to male	Type B	2.0 \pm 0.7 (N = 32)	
Male to female	Type A	4.6 \pm 1.1 (N = 74)	Females 209
Male to female	Type B	0.8 \pm 0.3 (N = 13)	
Female to male	Type A	5.0 \pm 1.4 (N = 164)	
Female to male	Type B	3.0 \pm 0.8 (N = 45)	
B. <i>Anolis extremus</i> adult males (N = 9) and females (N = 4)			
Male to male		11.2 \pm 1.8 (N = 101)	Males
Male to female		6.4 \pm 2.4 (N = 58)	159
Female to female		7.3 \pm 5.7 (N = 29)	Females
Female to male		9.8 \pm 5.9 (N = 39)	68
C. <i>Anolis leachi</i> adult males (N = 8) and females (N = 8)			
Male to male	Type A	24.3 \pm 10.6 (N = 194)	Males 498
Male to male	Type B	15.4 \pm 7.8 (N = 123)	
Male to female	Type A	14.1 \pm 5.3 (N = 113)	Females 663
Male to female	Type B	8.5 \pm 3.8 (N = 68)	
Female to male	Type A	9.5 \pm 6.2 (N = 76)	
Female to male	Type B	9.0 \pm 3.2 (N = 72)	
Female to female	Type A	41.3 \pm 19.1 (N = 330)	
Female to female	Type B	23.1 \pm 12.6 (N = 185)	

perience the same-sex context (*A. grahami*) or the same females did not produce displays in both contexts (*A. extremus*). Two few *A. leachi* subjects of either sex produced displays in both contexts to facilitate statistical tests. We used nested ANOVAs to assess the proportion of variation attributable to sex, among-subject and within-subject variance for each display unit (e.g., DeCourcy and Jenssen, 1994; Jenssen et al., 2000). For this analysis, all unit duration data for each subject were used rather than a mean value for each unit.

Statistical analyses were conducted with SPSS for Macintosh (vers. 10) except for the nested ANOVAs, which were run in a DOS environment with BIOM PC (F. J. Rohlf, BIOM: a package of statistical programs to accompany the text BIOMETRY. W. H. Freeman, New York, 1986). Sample sizes for displays analyzed are presented in Table 1. We follow Barlow's (1968) criterion for behavioral stereotypy, where display units having coefficients of variation (CVs) less than 35% are considered highly stereotyped.

RESULTS

Headbob displays in *A. grahami* comprised a series of "plateau-shaped" units, and two display types were performed, Type A and B (Jenssen, 1977b, 1981). These two display types are readily distinguished by differences in the duration of Units 2, 6, and 8: In Type B displays the duration of these units approaches zero (Ta-

ble 2; Fig. 1A–B). In practice, we used the duration of Unit 2 to classify displays as Type A or B, as this unit exhibits approximately an order of magnitude difference in duration between the two display types (Table 2; Jenssen, 1981). The first nine units in Type A displays (Fig. 1A) summed to approximately 3.7 sec in duration, whereas those in Type B displays (Fig. 1B) summed to about 3.0 sec (Table 2). In contrast, *A. extremus* produced only one type of stereotyped headbob display: a series of sinusoidal motions whose first 7 units summed to approximately 0.8 sec (Table 3; Fig. 1C).

Headbob displays of *A. leachi* differed from those of the other two species in several ways. First, displays always were performed in volleys (i.e., series) that ranged between about 7 and 12 sec in duration (mean = 8.6 \pm 0.34 sec; N = 16 subjects). Volleys contained two basic display types, which we termed Type A and Type B, that appeared in variable sequences and numbers of repetitions (Fig. 1D). Type A displays began with a rapid head drop, followed immediately with a rebounding head upswing and a second drop. Type B displays begin with a sharp head rise, followed by a brief pause, a sharp head drop, and a small rebounding rise.

Nested ANOVAs revealed the proportions of display variance attributable to signaler sex, among-subject variation within a sex class, and within-subject variation (Fig. 2). In *A. grahami* Type A displays, a subject's sex accounted for smallest amount of the variation (21.7%), fol-

TABLE 2. Between-sex comparisons of headbob displays from 16 adult male and six adult female *Anolis grahami* on Bermuda. Each subject contributed a mean value per parameter. Unit durations in seconds. Percent duration (% Dur) = a given unit's mean duration as a proportion of the sum of all unit mean durations for that display type. Test statistic is Mann-Whitney *U*. * Coefficient of variation (CV) unreliable when mean <0.1.

		Unit statistics								<i>U</i>	<i>P</i>
Display	Unit	Males (<i>N</i> = 16)				Females (<i>N</i> = 6)					
		Mean	SE	CV	% Dur	Mean	SE	CV	% Dur		
Type A	U1	1.230	0.132	43.1	32.4	0.899	0.035	9.5	25.0	16.0	.018
	U2	0.423	0.062	58.6	11.2	0.295	0.005	3.7	8.2	21.5	.051
	U3	0.327	0.016	19.1	8.6	0.253	0.018	17.2	7.0	15.0	.015
	U4	0.459	0.035	30.7	12.1	0.495	0.027	13.6	13.7	43.5	.740
	U5	0.349	0.014	16.6	9.2	0.285	0.013	11.2	7.9	14.5	.013
	U6	0.219	0.018	32.4	5.8	0.290	0.017	14.0	8.0	19.5	.036
	U7	0.384	0.023	23.5	10.1	0.411	0.037	22.2	11.4	43.0	.712
	U8	0.114	0.025	87.4	3.0	0.175	0.022	30.5	4.9	22.0	.055
	U9	0.286	0.023	32.0	7.5	0.501	0.037	18.1	13.9	00.0	.000
	U1-9	3.791	0.107	76.2	100.0	3.603	0.072	54.3	100.0	48.0	1.000
Type B	U1	1.158	0.066	20.7	36.9	0.905	0.051	13.8	31.2	14.0	.028
	U2*	0.048	0.031	—	1.5	0.042	0.020	—	1.4	27.5	.296
	U3	0.345	0.021	21.4	11.0	0.327	0.026	19.1	11.3	37.0	.861
	U4	0.446	0.067	54.0	14.2	0.495	0.042	20.9	17.1	38.5	.965
	U5	0.310	0.019	22.6	9.9	0.293	0.020	17.0	10.1	32.0	.539
	U6*	0.098	0.039	—	3.1	0.020	0.009	—	0.7	26.0	.246
	U7	0.410	0.028	24.9	13.0	0.426	0.017	10.0	14.7	31.5	.510
	U8*	0.012	0.005	—	0.4	0.017	0.014	—	0.6	38.0	.919
	U9	0.315	0.021	22.7	10.0	0.375	0.022	13.1	12.9	10.0	.035
	U1-9	3.142	0.114	98.1	100.0	2.899	0.095	88.3	100.0	20.0	.096

lowed by among-subject variance (27.7%), and within-subject variance (51.7%). Type B displays showed the same hierarchy in levels of variation: sex (6.4%), among-subject (33.8%), and within-subject (59.8%) variance. Although sex contributed least to the variation in both display types, that contribution was considerably greater in Type A than in Type B displays.

In *A. extremus* displays (Fig. 2C), subject sex accounted for the least amount of variation (7.1%), among-subject variance accounted for an intermediate amount of variation (23.3%), and within-subject variance accounted for most of the variation (69.6%). Virtually all of the vari-

ance in *A. leachi* displays could be attributed to within-subject variation (Type A displays: 98.9%; Type B displays: 99.3%).

Sex Effects on Display Temporal Structure.—In *A. grahami* Type A displays five of nine units (77.8%) differed significantly in duration between the sexes (with two additional units reaching $P < 0.06$), whereas only two of nine units (22.2%) differed significantly in Type B displays (Table 2). In total display duration (i.e., the sum of Units 1-9), neither display type differed significantly between the sexes (Table 2). However, females produced significantly more units per Type A display than did males (fe-

TABLE 3. Between-sex comparisons of headbob displays from nine adult male and four adult female *Anolis extremus* on Bermuda. Legend as in Table 2.

		Unit statistics								<i>U</i>	<i>P</i>
Unit		Males (<i>N</i> = 9)				Females (<i>N</i> = 4)					
		Mean	SE	CV	% Dur	Mean	SE	CV	% Dur		
	U1	0.254	0.010	11.8	32.0	0.251	0.013	10.1	31.0	17.5	.938
	U2*	0.016	0.004	—	2.0	0.047	0.011	—	5.8	2.5	.016
	U3	0.177	0.014	23.0	22.3	0.147	0.011	14.4	18.1	9.0	.165
	U4*	0.016	0.003	—	2.0	0.042	0.009	—	5.2	2.0	.013
	U5	0.172	0.008	14.4	21.7	0.169	0.007	8.1	20.9	14.0	.537
	U6*	0.054	0.018	—	6.8	0.037	0.001	—	4.5	8.5	.712
	U7	0.104	0.011	18.1	13.2	0.118	0.011	18.6	14.5	4.0	.480
	U1-7	0.793	0.034	80.4	100.0	0.810	0.030	69.3	100.0	6.0	.064

■ Between Sexes ▨ Among Subjects □ Within Subjects

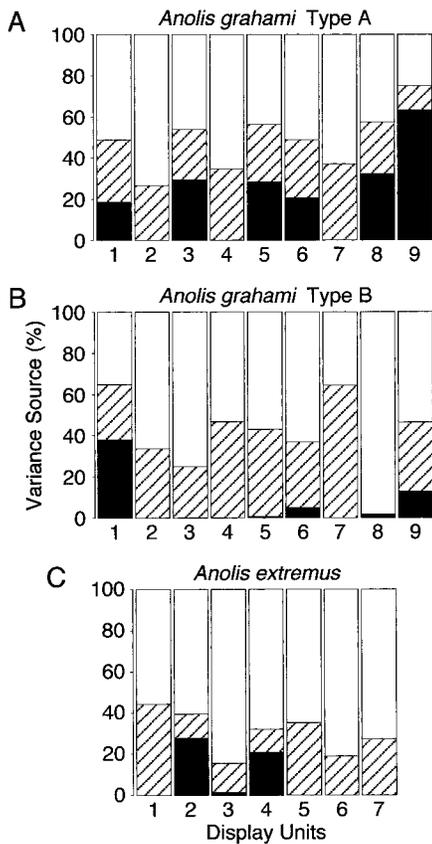


FIG. 2. Stacked bar graphs showing the proportion of variance in displays attributable in two-level nested ANOVAs to between-sex (black), among-subject (diagonal hatching), and within-subject (white) variation. (A) *Anolis grahami* Type A headbob display, (B) *A. grahami* Type B headbob display, (C) *Anolis extremus* headbob display.

male mean = 14.27 ± 1.17 sec, N = 6; male mean = 9.65 ± 0.23 sec, N = 16; U = 9, P = 0.004). A similar relationship was found for Type B displays (female mean = 16.59 ± 1.76 sec, N = 6; male mean = 11.13 ± 0.51 sec, N = 16; U = 4, P = 0.003). Taking both display types together, the CV was larger for males than fe-

males on all units for which this statistic could be calculated reliably (15 of 18 units total: Table 2).

In *A. extremus*, only two display units (28.6%) differed significantly in duration between the sexes, although total display duration (sum of Units 1–7) approached significance (Table 3). Like *A. grahami*, female *A. extremus* produced significantly more units per display than males (female mean = 8.24 ± 0.73 sec, N = 4; male mean = 5.03 ± 0.23 sec, N = 9; U = 0, P = 0.005). CVs were larger for males than females on three of the four units for which they could be calculated reliably (four of seven units total: Table 3).

Mean duration of *A. leachi* Type A displays was identical for both sexes, but differences in mean duration of Type B displays approached significance (Table 4). The quantity of Type A and B displays produced in volleys did not differ between the sexes (Type A displays: male mean = 6.88 ± 0.49, N = 8; female mean = 6.92 ± 0.55, N = 8, U = 30.5, P = 0.875; Type B displays: male mean = 6.52 ± 0.63, N = 8; female mean = 6.31 ± 0.50, N = 8, U = 31.5, P = 0.958. However, male volleys were significantly longer in duration than were female volleys (male mean = 9.47 ± 0.44 sec, N = 8; female mean = 7.73 ± 0.23 sec, N = 8; U = 4.0, P = 0.003). In Type A displays mean CVs for the two sexes were virtually identical, whereas males exhibited a slightly smaller mean CV for Type B displays (Table 4).

Context Effects on Display Temporal Structure.— In *A. grahami* Type A displays, unit durations did not differ significantly between male-male and male-female contexts (Table 5). Too few individuals produced Type B displays in both contexts to test for context effects. The number of units produced per display also did not differ between contexts (male-male: mean number of units = 9.69 ± 0.33; male-female: mean number of units = 9.77 ± 0.25; Wilcoxon Z = -0.169, P = 0.866, N = 8). In *A. extremus*, five display units were produced consistently in male-male and male-female contexts, but only one of these differed significantly in duration between contexts (Table 6). The number of display units pro-

TABLE 4. Between-sex comparisons on headbob displays from eight adult male and eight adult female *Anolis leachi* on Bermuda. Legend as in Table 2.

Display	Display statistics						U	P
	Males (N = 8)			Females (N = 8)				
	Mean	SE	CV	Mean	SE	CV		
Type A	0.311	0.013	11.5	0.311	0.013	11.8	30.0	0.834
Type B	0.348	0.012	9.8	0.308	0.014	12.4	14.5	0.066

TABLE 5. Differences in male *Anolis grahami* Type A headbob display unit durations between male-male and male-female contexts. Eight of 16 subjects contributed displays to both contexts. Test statistic is Wilcoxon *Z*.

Unit	<i>Z</i>	<i>P</i>
U1	-0.560	.575
U2	-0.840	.401
U3	-0.140	.889
U4	-1.260	.208
U5	-0.420	.674
U6	-0.560	.575
U7	-1.820	.069
U8	-0.840	.401
U9	-1.352	.176

duced did not differ between contexts (male-male: mean number of units = 4.61 ± 0.41 ; male-female: mean number of units = 4.93 ± 0.46 ; *Z* = -0.734, *P* = 0.463, *N* = 6).

Population Effects on Display Temporal Structure.—Neither display type of *A. grahami* males differed significantly in duration between the source population on Jamaica (data from Jensen, 1981:table 1) and the founder population on Bermuda (Type A display: Wilcoxon *Z* = -1.364, *P* = 0.173; Type B display: *Z* = -1.007, *P* = 0.314, *N* = 9 units). To compare other temporal attributes of the displays between the two populations we chose four basic parameters: units having the longest duration, shortest duration, largest CV, and smallest CV. None of these parameters differed between the two populations in Type A displays (Table 7). In Type B displays the two populations again exhibited the same longest- and shortest-duration units, but they differed in which units exhibited the largest and smallest CVs (Table 7).

For *A. extremus*, the range and mean number of display units produced was smaller in the Bermuda population (mean = 5, range = 3–7; *N* = 159 displays) than in the source population on Barbados (mean = 7, range = 3–9, *N* = 32 displays: data extrapolated from “peaks per bobbing sequence” in Gorman, 1968). Statistical comparisons were not possible due to the nature of these published data. No display data on Caribbean *A. leachi* were available for comparison to our study population on Bermuda.

DISCUSSION

Are Anolis Headbob Displays Sexually Dimorphic?—Our results suggest that, although some aspects of display temporal structure are sexually dimorphic, others are not. For example, female *A. grahami* and *A. extremus* both produced significantly more units per display than did conspecific males. In contrast, the presence of

TABLE 6. Differences in male *Anolis extremus* headbob display unit durations between male-male and male-female contexts. Six of nine subjects consistently produced displays of five units in both contexts. Test statistic is Wilcoxon *Z*.

Unit	<i>Z</i>	<i>P</i>
U1	-0.943	.345
U2	-2.023	.043
U3	-0.734	.463
U4	-1.782	.075
U5	-0.674	.500

sexual dimorphism in display unit durations varied with display type. Few sex differences were found in unit durations of *A. extremus* displays and in *A. grahami* Type B displays, but most units differed in duration between the sexes in *A. grahami* Type A displays. Sex differences in the total duration of displays approached significance for *A. extremus* and for *A. leachi* Type B (but not Type A) displays, and male volleys were significantly longer than female volleys in *A. leachi*.

By comparison, Jenssen et al. (2000) measured the duration of 24 units across three display types in *A. carolinensis* and found only four (about 17%) to differ significantly between the sexes. Nevertheless, one of three display types (Type B) differed significantly in total duration between the sexes (Jenssen et al., 2000). Stamps (1978), however, found no significant sex differences in the duration of headbob display units for the signature display of *Anolis aeneus*, a species closely related to *A. extremus* (Creer et al., 2001). As an example of other Iguania, Martins (1991) did not find sex differences in the duration of *Sceloporus graciosus* pushup displays, although males did produce significantly more headbobs per display than females. In sum, and despite among-species variation in which display parameters differed significantly between the sexes, most *Anolis* species whose displays have been scrutinized for sexual dimorphism have provided some level of support for it.

Do Sex Differences Exist in Anolis Display Stereotypy?—We predicted that stereotypy in headbob unit durations would be greater in males than in females, given the far greater importance of display to males (e.g., Jenssen et al., 2000). Our findings did not support this prediction. In virtually every case, unit durations were more variable in male than in female *A. grahami* and *A. extremus* displays. One possible explanation for this result is that increased variation in display unit durations could facilitate individual recognition among territory holding males. This seems unlikely, however, given that our nested ANOVAs revealed far greater within-

TABLE 7. Comparison of mean unit durations and coefficients of variation (CV) between *Anolis grahami* males from a founder population on Bermuda and from the source population on Jamaica. Founder population: 164 Type A and 45 Type B displays from 16 males (this study); source population: 84 Type A and 52 Type B displays from 16 males (from Jenssen, 1981). Highest values for each population in **bold** type with asterisks, and lowest values in *italics* with asterisks. Dashes indicate coefficient of variation (CV) unreliable when mean <0.1.

Unit	Type A displays				Type B displays			
	Mean unit duration (s)		Unit CV		Mean unit duration (s)		Unit CV	
	Founder	Source	Founder	Source	Founder	Source	Founder	Source
1	1.230*	0.905*	43%	19%	1.158*	1.000*	21%*	17%
2	0.423	0.585	59%	19%	0.048	<i>0.000*</i>	—	—
3	0.327	0.384	19%	20%	0.345	0.342	21%*	30%*
4	0.459	0.738	30%	24%	0.446	0.683	54%*	26%
5	0.349	0.298	17%*	16%*	0.310	0.316	23%	16%*
6	0.219	0.381	32%	21%	0.098	<i>0.000*</i>	—	—
7	0.384	0.433	24%	18%	0.410	0.415	25%	16%*
8	<i>0.114*</i>	<i>0.166*</i>	87%*	44%*	<i>0.012*</i>	<i>0.000*</i>	—	—
9	0.286	0.369	32%	24%	0.315	0.295	23%	25%
Total	3.791	4.259			3.142	3.051		

subject variation than between-subject variation in display unit durations. Moreover, a much simpler explanation exists. Our study included more than twice as many male *A. grahami* and *A. extremus* than females, and the larger coefficients of variation associated with male displays may stem from this sample size discrepancy. Support for this possibility comes from two sources.

First, our analysis of displays of *A. leachi* included eight adults of each sex, and for this species, the CVs of females were slightly higher than those of males (Table 4). Second, in a study of headbob displays of *A. carolinensis* that included 22 females and eight males, Jenssen et al. (2000) found female CVs to be larger than those of males in 20 of 24 units measured across three display types. In sum, if the coefficient of variation is as tightly linked to sample size as these comparisons suggest, its value as a measure of stereotypy clearly diminishes as sample size sex bias increases.

Does Context Influence Anolis Display Temporal Structure?—We examined the possibility that context influenced display structure by comparing displays produced by the same males in male-male and male-female encounters. Our analysis revealed a context effect on display unit duration for only one unit of 14 examined (Tables 5–6), and failed to show any effect of context on the mean number of units produced in displays.

By comparison, the potential effect of context on display temporal structure was investigated in two laboratory studies of headbob displays of *A. carolinensis* using nested ANOVAs. Including in their analysis factors for display type,

context (male-alone and male-male), among-subject, and within-subject variation, DeCourcy and Jenssen (1994) found context to account for less than 4% of the variance in display structure. Similarly, in an examination of male display structure across three populations, Lovern et al. (1999) included factors for population, context (male-alone, male-male, and male-female), among-subject variation, and within-subject variation. Context was found to account for an average of about 7% of the variance in display structure. These results are consistent with our findings that display context had only a subtle influence on the structure of displays of *Anolis*.

Does Anolis Display Structure Vary at the Population Level?—We tested whether mean unit durations differed between the headbob displays of *A. grahami* source (Kingston, Jamaica) and founder (Bermuda) populations but were unable to detect a significant difference. We also examined four parameters characterizing the major temporal attributes of the displays: the longest and shortest units, and the units with the largest and smallest CVs. Except for the largest and smallest CV values in Type B displays, the two populations did not differ on the parameters examined.

Gorman et al. (1976) considered the roughly 18% reduction in heterozygosity in *A. grahami* on Bermuda (compared to their source population) to be relatively minor, and attributed this fact to the unusually large founder population. Likewise, our findings for *A. grahami* suggest that the temporal patterning and stereotypy in headbob displays have changed little in nearly a century of separation from the source population.

This stability in display structure likewise has been noted in another study of anole introductions. Lovern et al. (1999) compared the headbob displays of *A. carolinensis* introduced to Hawaii around 1950 with those of endemic *A. carolinensis* in Florida and Georgia. Although some significant differences in display unit durations were found across the three populations, the Hawaiian founder population deviated no more from the two endemic populations in unit durations or CVs than the two endemic populations deviated from each other. In fact, the introduced Hawaiian population was more similar in display structure to the population from Georgia than the latter was to conspecifics in the adjacent state of Florida (Lovern et al., 1999).

In striking contrast, the first four of nine headbob display units from two *A. nebulosus* populations, located approximately 250 km apart in Mexico, exhibited virtually no overlap in duration (Jenssen, 1971). Similarly large population-level differences have been described for other members of the Iguania. For example, Ferguson (1970) and McKinney (1971) documented considerable population differences in headbob display structure of *Uta stansburiana* involving unit durations and the total number of units produced per display. Likewise, Martins et al. (1998) found significant population differences in the number of units produced in displays by *Sceloporus graciosus* from Utah, Oregon, and southern California. Generally speaking, these studies compared populations separated by considerable (but contiguous) geographic distances and most likely by substantial expanses of time. Display structure differences of equivalent magnitude, for example, have been shown for *A. grahamsi* populations separated by millions of years on Jamaica (Jenssen, 1981; Macedonia and Clark, 2001; Jackman et al., 2002). Accordingly, comparisons of populations separated in time by thousands or millions of years might reasonably be expected to exhibit more dramatic differences than those anticipated between populations isolated by only 50–100 years (e.g., this study; Lovern et al., 1999).

Nevertheless, results from a comparative study of rock iguanas (*Cyclura*) suggest that large differences in display structure can arise in a short time. Martins and Lamont (1988) compared headbob displays from the source population of *Cyclura nubila nubila* on Cuba with those from descendants of several individuals that escaped from a zoo on Puerto Rico in the early 1960s. The mean duration of display units involving motion (cf. pauses) in the founder population was observed to be about 350% greater than in the source population. Moreover, this difference in display temporal structure evolved in only about six generations (Martins

and Lamont, 1988). By comparison, the same display units in *Cyclura nubila lewisi* from Grand Cayman differed from those of *C. n. nubila* on Cuba by only about 20%. Although the size of the founding population of *C. n. lewisi* on Grand Cayman cannot be estimated, the rapid change in display structure in *C. n. nubila* on Puerto Rico illustrates the potential of small founding population size as a catalyst to display evolution.

As a final example, Macedonia and Clark (2001) documented differences in headbob displays among three "color" populations (green, brown, and blue) of the Grand Cayman anole (*Anolis conspersus*), which shares a most recent common ancestor with the "Kingston" population of *A. grahamsi* (Jackman et al., 2002). The distribution of the blue morph is contiguous with those of the green and brown morphs, whereas the latter two populations are allopatric. Each color population differed significantly from one or more of the others in display unit durations, and the brown form was the most distinctive. Although significant, the differences in unit durations among these color populations were subtle. In that sense, they were more similar in magnitude to intraspecific sex differences shown in the present study than to some of the comparisons described above for conspecific populations separated by large geographic distances.

Given that Gorman et al. (1976) found genetic heterozygosity in *A. extremus* on Bermuda to be only about 16% that of the source population on Barbados, we anticipated that we would document differences in display structure between the two populations of this species. Unfortunately, the published display data available for the Barbados population constrained our comparison to the mean number and range of units produced in displays, which did appear to differ between the two populations. Acquiring detailed display data from *A. extremus* on Barbados in the future would permit a closer examination of display structure in two conspecific populations that differ dramatically in genetic variability.

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