

## Headbob Display Analysis of the Grand Cayman Anole, *Anolis conspersus*

JOSEPH M. MACEDONIA<sup>1,2</sup> AND DAVID L. CLARK<sup>3</sup>

<sup>1</sup>Center for the Integrative Study of Animal Behavior, Indiana University, Bloomington,  
Indiana 47405, USA

<sup>3</sup>Department of Biology, Alma College, Alma, Michigan 48801, USA

**ABSTRACT.**—Headbob displays from 22 adult male *Anolis conspersus* of three “color morphs” (green, brown, and blue) were videotaped in the laboratory. Frame-by-frame coordinates of the vertical head motions were used to generate display-action-pattern (DAP) graphs. Field observations had revealed that only one type of headbob display (“Type A”) was performed when males displayed to nonspecific audiences while moving around their territories (“male-alone context”). During staged male encounters in the lab (“male-male context”), Type A displays and a second type of display (“Type B”) were produced. The two types of displays were partitioned into units that were compared among the color morphs. We then transformed the display units with principle components analysis and used one-way ANOVAs to test statistically for differences among the color morphs at the “unit” level. Finally, we used discriminant function analysis to test for color morph differences at the “display” level. Graphical visualization and statistical analyses showed that, like body coloration, the green and the brown morph are more distinctive from each other than either is from the blue morph, although the differences in display units among the color forms are subtle. Given that *A. conspersus* is a member of the seven-species *Anolis* radiation on Jamaica, we compare the structure of one of its displays (Type A) with that of its closest relative, *Anolis grahami*. Last, we speculate on the possible origin of the unusual display structure observed in the *A. conspersus* Type B display.

Many species of lizards have evolved motion and color displays that are used in signaling to potential mates, conspecific rivals, and predators (e.g., Carpenter and Ferguson, 1977; Hasson et al., 1989; Cooper and Greenberg, 1992; Leal and Rodriguez-Robles, 1997). *Anolis* is one of several diverse lizard genera whose displays have received focused research attention (e.g., Jenssen, 1977; Fleishman, 1992; Macedonia and Stamps, 1994). Although display structure has been described for a number of *Anolis* species (e.g., Jenssen, 1978), signal characteristics, such as headbobbing patterns or dewlap colors, have been compared among populations of only a few species (e.g., Jenssen, 1971, 1981; Christman, 1980; Jenssen and Gladson, 1984; Case, 1990; Lovern et al., 1999).

*Anolis conspersus* is the only non-Jamaican member of a seven-species monophyletic radiation known as the “*grahami* series” (Williams, 1976). Within this series, *A. conspersus* belongs to the four-species “*grahami* group” clade (Hedges and Burnell, 1990; T. Jackman, D. J. Irschick, K. de Querioz, J. B. Losos, and A. Larson, unpubl.). This arboreal lizard is endemic to Grand Cayman and is the only fossil anole known from the island (e.g., Morgan, 1994). De-

spite the fact that Grand Cayman is small, low lying, and only about 35 km in length, *A. conspersus* exhibits differences in coloration at the population level. Although dewlap color variation is relatively minor (the dewlap is blue and highly UV-reflective in all populations), three different body-color morphs have evolved: green, brown, and blue (Macedonia, 1999; Macedonia et al., 2000).

Aside from one illustration (Macedonia and Stamps, 1994), no data on the headbob displays of *A. conspersus* have been published. Given that the geographic distributions of the color forms correspond to rainfall-related habitat differences (Macedonia, 1999; JMM, unpubl. data), we sought to determine whether headbob displays differ among these morphs as well. We predicted that, if present, these differences would be largest between the green and the brown morphs—the two populations separated by the greatest geographic distance (Fig. 1).

In this paper, we have three primary aims. First, we quantify headbob displays of male *A. conspersus*, a species for which such data do not currently exist. Second, we compare our results among the three color morphs to determine whether, like color, differences in displays also are present at the population level. Last, we compare the structure of *A. conspersus* headbob displays to those of this species’ close phylogenetic relatives on Jamaica, and we discuss some implications of the shared signal structures.

<sup>2</sup> Present Address: Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996-1610, USA; E-mail: jmacedon@utk.edu.

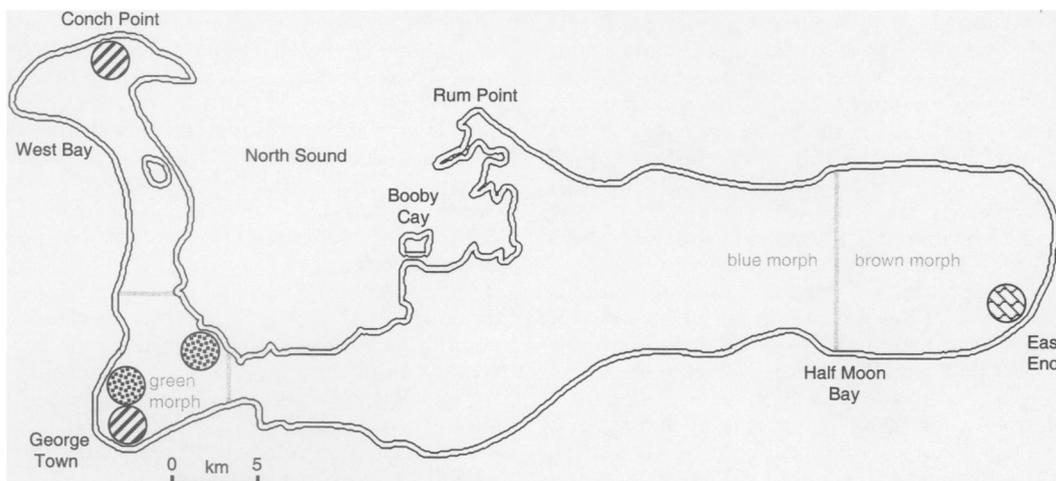


FIG. 1. Map of Grand Cayman with color morph collection sites shown: circles with square dots = green morph (*Anolis conspersus conspersus*); circle with "brick" hatching = brown morph (*Anolis conspersus lewisi*); circles with diagonal lines = blue morph (unnamed taxon). Thick gray lines to the east and northwest of George Town indicate the approximate limits of the green morph distribution. Thick gray line running from Half Moon Bay (Frank Sound) to the northern coast approximates the eastern limit of the blue morph and western limit of the brown morph.

#### MATERIALS AND METHODS

**Study Populations.**—We use the term "green morph" to refer to the subspecies *A. conspersus conspersus* (Grant, 1940). The dorsum, legs, and tail are yellowish-green with an overlying pattern of dots to vermiculations; the sides are a bluish-green; and the yellowish-green head can be more yellow than green in some geographic locations. This morph appears to be restricted largely to the southwestern corner of Grand Cayman (i.e., George Town; Fig. 1). However, a "light green" population apparently exists on Booby Cay, a small islet adjacent to the central mangrove habitat on the west side of the North Sound (Grant, 1940).

The "brown morph" refers to the subspecies *A. c. lewisi* (Grant, 1940). The head, dorsum, and sides are medium brown; the tail is turquoise; and the legs can be either brown or brownish-blue. Most individuals have an overlying pattern of vermiculations (not dots). On occasion, entirely "beige" individuals are seen, usually (but not always) with overlying vermiculations (pers. obs.). The brown morph is restricted to the eastern one-quarter of the island, roughly along a longitudinal transect running from Half Moon Bay (Frank Sound) on the south shore northward (Fig. 1).

Over much of the rest of Grand Cayman, a taxonomically unrecognized "blue morph" occurs whose distribution abuts and in some locations infuses those of the green and brown morphs. This morph is quite variable in coloration, both within and among geographic loca-

tions. We have found adult males with yellow-green snouts, as well as individuals that exhibited different combinations of green and brown morph coloration traits. Typical members of this population exist, however, and are turquoise with light dots (not vermiculations), have blue or turquoise legs; and the entire dorsal surface exhibits a wash of dark brown. The blue morph might possibly be a nonvermiculate (dotted) and reduced-melanin variant of the brown morph that, upon expanding its distribution to western Grand Cayman, has interbred to varying extents with the green morph. Because population genetic profiles are unknown for any of the color morphs, one can only speculate about the actual identity of the blue morph. Nevertheless, because the blue morph does not fit comfortably within the color pattern variations observed in either the green or brown morphs, we treat it here as its own entity. The blue morph subjects in this study came from two locations where among-subject color variation was small (Fig. 1) and individuals were of "morph-typical" coloration.

**Subjects and Housing.**—Adult male *A. conspersus* were collected on Grand Cayman in January 1993 and June 1997. The animals collected in 1993 were housed temporarily at facilities located at the University of California, Davis, then moved to Alma College, Alma, Michigan, in August 1993, where videotaped data on headbob displays were gathered. The animals collected in 1997 were housed and videotaped at Indiana University, Bloomington, Indiana.

All lizards were maintained on a 14:10 L:D light cycle, 40–50% relative humidity, and a temperature of 26–29°C. Lighting was provided by full-spectrum fluorescent lights mounted on the ceiling and walls of the room. Each subject was housed individually in a clear plastic cage (28 cm × 17 cm × 19 cm) furnished with a wooden dowel as a perch. The anoles were misted daily and fed vitamin- and calcium-dusted crickets every 2–3 days.

*Data Acquisition.*—*Anolis conspersus* exhibits two types of headbob displays, which we refer to as "Type A" and "Type B." We follow the convention (e.g., Jenssen, 1977) that the headbob display pattern exhibited in the "male-alone" (formerly "assertion") context is labeled Type A. We label an additional headbob display pattern Type B, which, in addition to Type A, is observed in the "male-male" (formerly "challenge") context (e.g., DeCourcy and Jenssen, 1994).

In 1993, displays were recorded during staged contests between pairs of green morph males in wooden observation chambers (180 cm × 39 cm × 44 cm) modeled after those illustrated in DeCourcy and Jenssen (1994). Interactions were recorded with two Panasonic (PV-7100) camcorders, with each camcorder following one subject. A "screen-splitter" (Panasonic WJ-MX10 digital AV mixer) was used to combine the two video images onto a single videotape, and a Panasonic WV-KB12A character generator stamped the date and time onto the tapes. Contests were videotaped from behind a cloth blind, with small openings cut to accommodate the camcorder lenses.

An x-y coordinate system (DeluxePaint IV, Electronic Arts) was superimposed over the video image of a displaying lizard using the internal genlock (a device used to combine a video and computer-generated image) in an Amiga 3000 ("VideoToaster"). A cursor was placed over the image of the lizard's eye and vertical coordinates of head motion were read off the screen and transcribed manually frame-by-frame (30 frames/sec). The changes in coordinates were compiled and graphed using CricketGraph (Cricket Software). Displays whose measurement accuracy might be compromised by the subject's orientation in the cage were not used (e.g., if a subject was positioned such that its head moved toward and away from the camera during a display).

In 1997, displays were elicited from all three color morphs by placing a subject's cage in front of a mirror and videotaping the response for as long as the subject would display toward the mirror. Displays occurring in this manner were considered to be performed in the male-male context and were recorded with a Canon L1 Hi8

camcorder before being copied to Mini DV tape using a Sony DHR-1000 digital videocassette recorder. These tapes were played through the A/D card of a Power Macintosh 8600/300 computer using the single-frame advance feature of the DV recorder and the public domain video analysis software, NIH Image (<http://rsb.info.nih.gov/nih-image>). Vertical coordinates of head motion were transcribed to data sheets as described above.

Display-Action-Pattern (DAP) graphs (e.g., Carpenter, 1962; Jenssen, 1978) were divided into odd- and even-numbered units. By convention, odd-numbered units designate headbobbing movements, whereas even-numbered units indicate pauses. Unit lengths for each display were calculated by referring to printouts of the coordinates used to generate the DAP graphs. Unit length data then were converted to durations.

*Descriptive Statistics.*—Descriptive statistics were calculated to include mean, standard error (SE), and the coefficient of variation (CV), as well as the percent duration of each unit as a proportion of the total display. Like Jenssen (e.g., 1978), we follow Barlow's (1968) criterion of behavioral stereotypy in considering headbob units with CVs less than 35% to qualify as "stereotyped."

*Principle Components Analysis.*—Exploratory data analyses revealed that many display units were correlated and nonnormally distributed. Therefore, we conducted a principle components analysis (PCA) separately for Type A and Type B displays to account for the maximum amount of variation in the dataset with several normally distributed and uncorrelated variables. To increase interpretability, the components were rotated orthogonally to ensure high correlations with as few of the original variables as possible (e.g., Kleinbaum and Kupper, 1978).

*Population Differences in Displays.*—Two approaches were taken to determine whether differences in displays exist among the three *A. conspersus* populations (color morphs). First, one-way ANOVAs were run on principle components whose eigenvalues were > 0.7 (Jolliffe, 1986). When ANOVAs were significant, protected (Bonferroni) pairwise tests were carried out.

Second, principle components for each display pattern were entered into a discriminant (canonical) function analysis (DFA) to determine the accuracy with which the functions could assign a given display to the correct *A. conspersus* color morph. Scores from all components (nine components for Type A displays and four for Type B) were entered into the analysis to avoid excluding those components, which, despite accounting for less overall variation, might contain important among-group (color morph) discrim-

TABLE 1. Sample sizes for Type A and Type B headbob displays of 22 adult male *Anolis conspersus* as grouped by color morph: green morph = *Anolis conspersus conspersus*, brown morph = *Anolis conspersus lewisi*, blue morph = taxonomically unrecognized.

Subject	Green morph		Brown morph		Blue morph	
	A	B	A	B	A	B
1	8	16	5	27	14	29
2	5	27	6	8	11	13
3	6	10	7	17	7	24
4	10	20	4	0	11	19
5	30	12	0	17	6	23
6	18	34			11	36
7	0	11			0	7
8	0	16				
9	0	21				
10	0	17				
Total	77	184	22	69	60	151

inatory power. To avoid biasing function construction in favor of those color morphs for which we had larger sample sizes (Table 1), 20 component scores were chosen in a constrained random fashion for Type A displays and 60 component scores for Type B displays. Our constraint was for each subject to contribute, as closely as possible, an equal number of component scores to the analysis. For example, to obtain 20 component scores from six subjects, four subjects would contribute three component scores each (total = 12 scores) and two subjects would contribute four component scores each (total = 8 scores). Which component scores were chosen from each subject was random. The functions that were generated then classified the component scores (each score being equivalent to one display) as belonging to one color morph or another in a "blind" fashion. Chi-squared tests were used to determine whether classification assignments differed significantly from chance. Statistical analyses were conducted with SPSS for Macintosh (vers. 6.1).

## RESULTS

*Display Description and Stereotypy.*—Type A displays of *A. conspersus* contained between five and 13 units. We arbitrarily required a minimum of seven units for a display to be included in our quantitative analyses. Durations were measured for the first (seven to) nine units so that unit-by-unit comparisons could be made with Jenssen's (1981) data for the same display patterns of other *grahami* group members.

Type B displays were divided into three units: Unit 1 is a quick "up-down" motion (seen graphically as a "spike") with the head returning to its starting position; Unit 2 is a brief pause; and Unit 3 is a larger amplitude "down-

TABLE 2. Descriptive statistics for display units from 22 adult male *Anolis conspersus* in this study. Unit 4 (U4) of the Type B display separates displays in a volley and is not part of the headbob pattern, per se. Unit durations are in seconds. Percent duration (% Dur) = a given unit's duration as a proportion of the sum of all unit durations in the table for that display type. For Type B displays, % Duration is calculated both with and without Unit 4.

Display	Unit	Mean(s)	SE	CV	% Dur	% Dur w/o 'U4'
Type A	U1	0.749	0.023	12.7	33.4	
(N = 159)	U2	0.565	0.019	14.1	25.2	
	U3	0.134	0.005	15.9	6.0	
	U4	0.297	0.021	29.3	13.3	
	U5	0.122	0.004	12.7	5.4	
	U6	0.105	0.018	70.5	4.7	
	U7	0.123	0.004	14.2	5.5	
	U8	0.030	0.011	153.8	1.3	
	U9	0.116	0.016	27.6	5.2	
Type B	U1	0.133	0.010	34.6	9.4	24.8
(N = 404)	U2	0.160	0.026	74.1	11.3	29.9
	U3	0.243	0.011	20.1	17.2	45.3
	U4	0.878	0.042	21.9	62.1	

up-down" motion with the head returning to its initial position on the final downswing. What we have designated as "Unit 4" is not a unit, per se, but is the pause between displays in "volleys" (i.e., a series of displays performed in continuous succession). Because virtually all Type B displays occur in volleys, this pause between displays was included in our quantification of unit durations.

For Type A and Type B displays a single dewlap pulse (i.e., extension/retraction) often is performed just prior to the onset of a headbob display, and one or more dewlap pulses may follow a headbob display. When performed in volleys, a single dewlap extension is begun as a headbob is ending, and the dewlap's retraction is nearly complete as the next headbob in the series is begun (see Macedonia and Stamps, 1994).

For Type A displays, five of the nine units measured exhibited CVs of less than 20% and only two units (Units 6 and 8, both pauses) exhibited CVs greater than 35% (Table 2; Fig. 2a). Type B displays were similarly stereotyped, with only Unit 2 (a pause) being highly variable (Table 2; Fig. 2b).

Type A displays were most often produced in pairs (mean = 2.2 displays/volley, SD = 1.7, N = 156 volleys), whereas Type B displays were almost always performed in long volleys (mean = 6.8 displays/volley, SD = 3.3, N = 159 volleys). Subjects produced significantly more Type B (N = 1459, 78%) than Type A (N = 414, 22%) displays (N = 22 subjects, Wilcoxon Z = 4.109, P = 0.0001). Despite differences in the du-

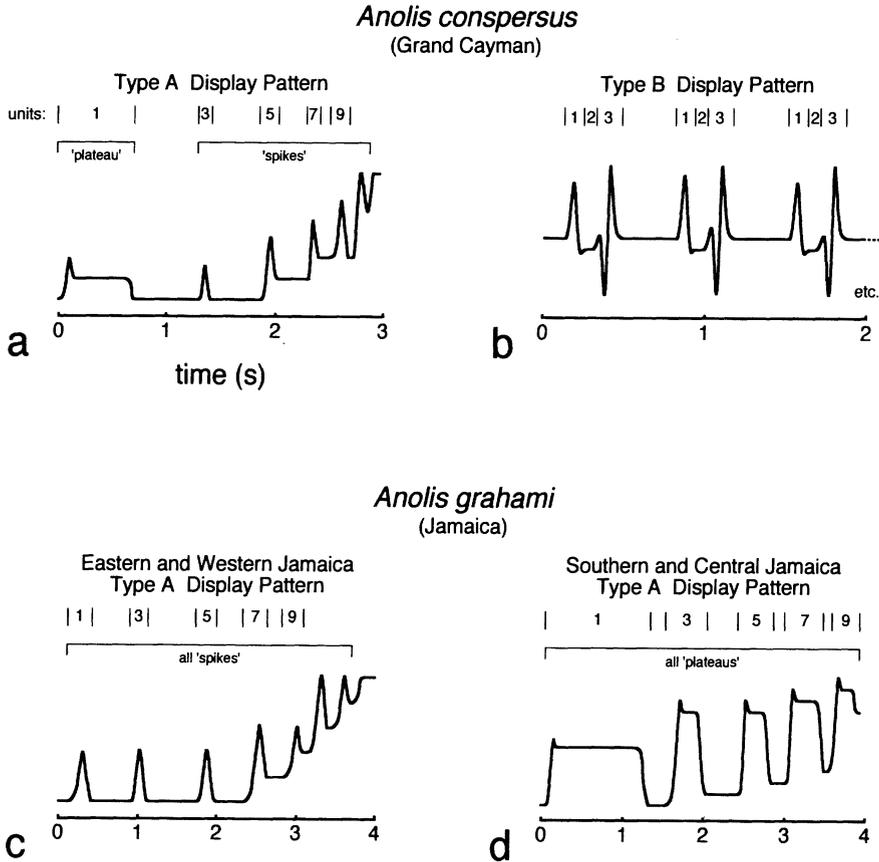


FIG. 2. Representative headbob displays from *Anolis conspersus* and *Anolis grahami*. (a) Type A display of *A. conspersus*; (b) volley of three Type B displays of *A. conspersus*; (c) Type A display with "spike-shaped" units characteristic of the *A. grahami* population from eastern and western Jamaica; (d) Type A display with "plateau-shaped" units characteristic of the *A. grahami* population from southern and central Jamaica.

rations of the two display patterns (Type A: sum of unit means = 0.536 s,  $N = 404$  displays; Type B: sum of unit means = 2.241 s,  $N = 159$  displays), the total amount of time spent producing Type A and B displays did not differ ( $N = 22$ ; Wilcoxon  $Z = -0.99$ ; NS).

*Headbob Display Variability among Populations.*—Differences in unit durations among the three color morphs were relatively subtle, with the values of the blue morph unit durations being intermediate between those of the green and brown morphs (although slightly more similar to the green morph: Fig. 3). Two attributes of brown morph displays that are relatively apparent, however, are the absence of a Unit 8 in the Type A display and a comparatively brief Unit 2 in the Type B display (Fig. 3).

To gauge the magnitude of color morph display differences statistically, unit durations were transformed to principle components scores. Following axis rotation, the components generated for Type A displays exhibited relatively

simple structure, that is, they were weighted heavily on one or, at most, two display units (Fig. 4). The components generated for Type B displays exhibited even stronger simple structure after rotation, each being weighted approximately 99% on a single display unit (Fig. 5).

To quantify display differences among the color morphs with these "restructured" display units, we ran one-way ANOVAs on those components that exceeded Jolliffe's criterion (the first six components for Type A displays and the first three components for Type B displays). All components except PC4 (roughly equivalent to Unit 5; see Fig. 4) differed significantly among the color morphs in Type A displays (Table 3). Protected pairwise tests revealed that four of six significant differences were between the green and brown morph. For Type B displays, all three components tested differed significantly among the color morphs (Table 3).

Last, we used discriminant (canonical) functions analysis to test for differences among the

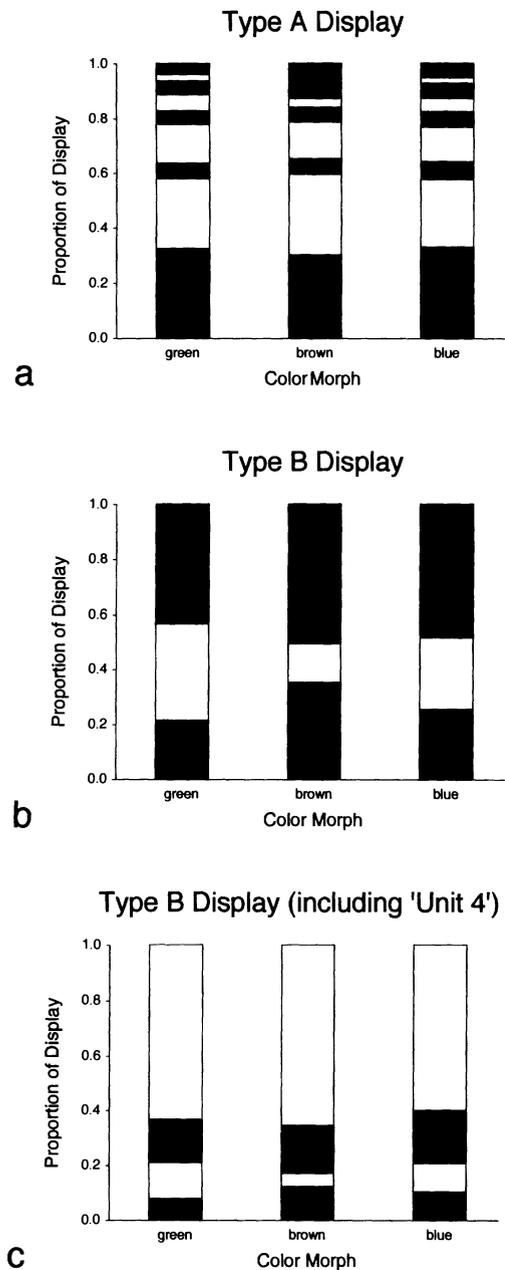


FIG. 3. Stacked bar graphs showing unit durations in (a) Type A and (b) Type B headbob displays from the three *Anolis conspersus* color morphs. Unit 1 is at the bottom of each bar, and subsequent units are stacked in tandem. (c) "Unit 4" refers to the pause between Type B displays during the volleys (series) in which they are performed.

color morphs at the level of entire displays. For Type A and Type B displays, classification assignments were significantly greater than chance for the green and the brown morph but not for the blue morph (Table 4). In addition, the

number of brown morph scores incorrectly assigned to the green morph was significantly less than chance. These results indicate that green and brown morph headbob displays were sufficiently distinctive to be reliably discriminated by functions tailored to perform that task. In contrast, the blue morph did not exhibit an equivalent level of discriminability. It is worth noting, however, that one additional correct classification in the Type A (but not Type B) displays of the blue morph would have produced significance (at  $\alpha = 0.05$ ).

#### DISCUSSION

*Display Description and Stereotypy.*—*Anolis conspersus* exhibits two types of headbob displays, Type A and Type B. In the male-alone context (not analyzed in this paper), only the Type A pattern is observed. In the male-male context, both Type A and Type B occur. Both types of displays were stereotyped for nearly all units (seven of nine Type A units and three of four Type B units exhibited CVs less than 35%). Until *A. sagrei* appeared on Grand Cayman in the early 1980s (Minton and Minton, 1984), *A. conspersus* was the sole *Anolis* species known from the island. Thus, selection for species recognition has not been the force responsible for maintaining this stereotypy in the absence of congeners.

*Headbob Display Variability among Populations.*—In addition to body coloration, headbob display structure also differed among the three color morphs. This variation is subtle and appears to be limited to differences in unit durations among the populations. Interestingly, McKinney (1971a) also found that differences in body coloration among populations of *Uta stansburiana* across the western and southwestern United States that usually were accompanied by differences in headbob display patterns.

It is possible that there are additional display differences among the *A. conspersus* color morphs that we did not measure. For example, Ferguson (1970) and McKinney (1971b) showed that population differences in *U. stansburiana* headbob display structure involved not only unit durations but also the total number of units produced per display and relative head height of different units. Similarly, Martins et al. (1998) found population differences in number of headbob units produced by *Sceloporus graciosus* from Utah, Oregon, and southern California, as well as in other variables such as the number of legs extended when displaying and the use of postures accompanying the displays.

Nevertheless, there are some interesting parallels between the comparatively small geographic distances among the *A. conspersus* color morphs and the differences found in headbob

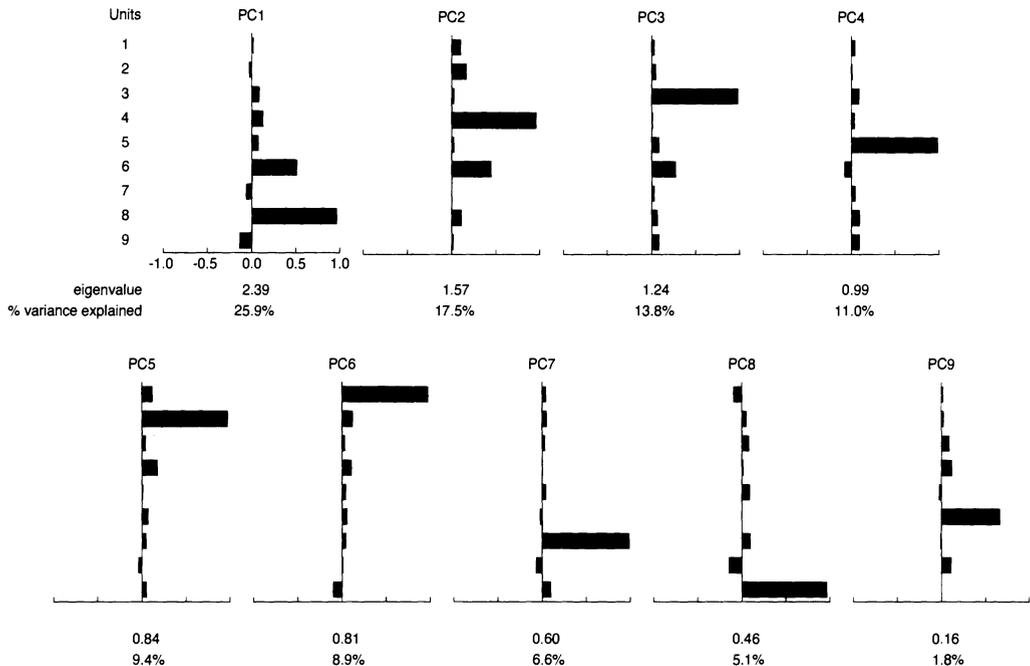
Component Loadings from PCA of *A. conspersus* Type A Display Units

FIG. 4. Component loadings from a principle components analysis on the nine units of *Anolis conspersus* Type A displays (color morphs combined). The loadings are correlations between the original variables and the components derived from them. Eigenvalues (quantity of variance explained) and percent variance explained are shown beneath the loadings of each component.

display structure. The geographic distributions of the green and the brown morphs do not overlap spatially, and thus, there may be little to no gene flow between populations. Therefore, it follows from our prediction that the greatest differences in unit durations (and transforms of those units, Tables 3–4) would be observed between these two color morphs. In contrast, the blue morph is the most variable in body coloration and can possess coloration attributes of the green and the brown morphs. Likewise, the blue morph is intermediate to, and least distinctive from, the green and brown morphs in temporal aspects of headbob displays.

This combination of color and display distinctiveness of the green and brown morphs, and the intermediacy of the blue morph, presents a good case for a population genetics study. As far as we can determine, there is no mention of the blue morph in the literature, and as recently as 60 yr ago, *A. conspersus* from western Grand Cayman were, apparently, green. B. Lewis (as quoted in Grant, 1940:25) terms the coloration of our green morph from George Town "bright grass green," but also states that "In the West Bay area . . . [the lizards] can easily be recognized from the George Town popula-

tion by their yellow-green color." Today, only the blue morph occurs in West Bay.

Last, similar to our results, Lovern et al. (1999) examined three populations of *A. carolinensis* and found subtle but statistically reliable differences in most headbob display units. Like the present study, significance stemmed primarily from low within-unit temporal variance (i.e., stereotypy) rather than coarse interpopulation differences in unit durations.

*Comparison to Other Grahams Group Members.*— We compared attributes of the *A. conspersus* Type A display (color morphs combined) with displays quantified by Jenssen (1981) for adult males of two *A. grahami* populations and for one *A. garmani* population, as well as with our own data on a population of *A. opalinus* (the remaining *grahami* group member). Jenssen (1981) filmed his subjects in two environments (field and laboratory) and in two social contexts (male alone and male-male), whereas our subjects were videotaped only in the lab and only in the male-male context. It is important to note that tests for potential environmental and contextual influences on display structure have failed to find an effect of these variables (Lovern et al., 1999). Earlier studies (Jenssen, 1971; Jenssen and

### Component Loadings from PCA of *A. conspersus* Type B Display Units

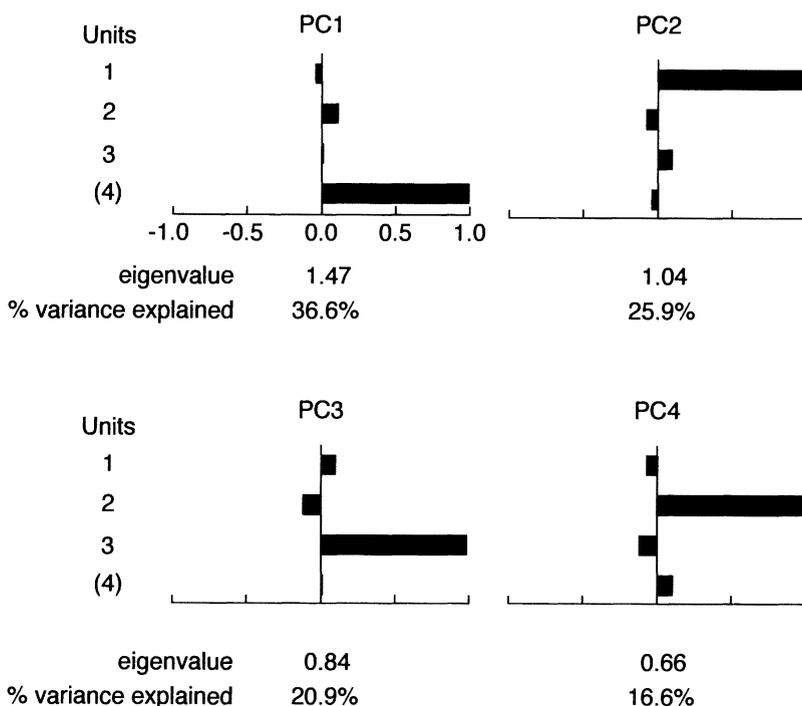


FIG. 5. Component loadings from a principle components analysis on the four units of *Anolis conspersus* Type B displays (color morphs combined). Legend as in Figure 4.

TABLE 3. One-way ANOVAs on principle component scores for Type A and Type B displays, as grouped by color morph. Degrees of freedom: between groups = 2, within groups = 156 (Type A), and 401 (Type B). Asterisks indicate significance at  $P < 0.05$  in protected (Bonferroni) pairwise comparisons. Only those components exceeding Jolliffe's (1986) criterion (eigenvalues  $> 0.7$ ) were used (see text).

PC	F-ratio	P	Green vs. brown	Green vs. blue	Brown vs. blue
<b>Type A</b>					
1	7.272	0.0010	*		
2	7.748	0.0006		*	*
3	5.443	0.0052	*		
4	1.521	NS			
5	4.051	0.0193	*		
6	4.498	0.0126	*		
<b>Type B</b>					
1	16.470	0.0000	*	*	
2	6.689	0.0014		*	
3	9.838	0.0001	*		*

TABLE 4. Discriminant function (canonical) analysis classification assignments of principle components scores from Type A and Type B displays. Significance levels for chi-squared tests of DFA classification assignments indicated as: \*\*\* =  $P < 0.001$ , \*\* =  $P < 0.01$ , \* =  $0.02 < P < 0.05$ . Note that significance can be "greater than" or "less than" chance.

Display type	Actual color morph	N	Predicted color morph		
			Green	Brown	Blue
A	Green	20	13	2	5
		%	65.0%*	10.0%	25.0%
	Brown	20	1	15	4
	%	5.0%	75.0%**	20.0%	
	Blue	20	5	3	12
	%	25.0%	15.0%	60.0%	
B	Green	60	34	10	16
		%	56.7%**	16.7%	26.7%
	Brown	60	7	42	11
	%	11.7%**	70.0***	18.3%	
	Blue	60	22	14	24
	%	36.7%	23.3%	40.0%	

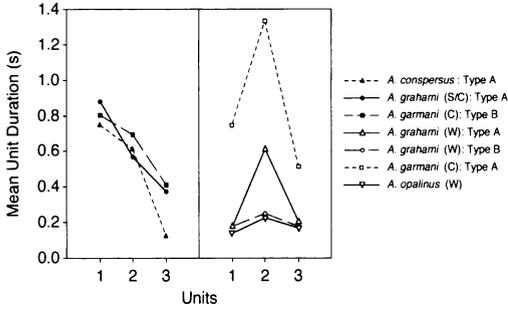


FIG. 6. Comparison of display temporal patterns in the four *grahami* group species. Mean durations for the first three display units are shown for *Anolis grahami* ( $N = 21$ ), *Anolis conspersus* ( $N = 22$ ), *Anolis garmani* ( $N = 3$ ), and *Anolis opalinus* ( $N = 6$ ). For the two *A. grahami* populations illustrated, S&C = southern (Kingston) plus central (Mandeville) subjects ( $N = 16$ ), and W = western (Negril) subjects ( $N = 5$ ). The *A. garmani* population was from Mandeville (C) and the *A. opalinus* population was from Discovery Bay (W). Data for species/populations other than *A. conspersus* and *A. opalinus* were taken from Jenssen (1981). The Type B display of *A. conspersus* is unique within the *grahami* group and cannot be meaningfully compared here (see Fig. 2). Type B display of S&C *A. grahami* lacks a Unit 2 and likewise must be excluded from this comparison. (Note: "Type A" and "Type B" are merely labels by which to identify display types within a species.)

Gladson, 1984) also corroborate the inability to detect a "laboratory effect" of displays performed in unnatural surroundings. Therefore, we are confident that the results of unit-by-unit display comparisons between our datasets and those of Jenssen (1981) are reliable.

A consistent temporal pattern in display structure was observed in the relative durations of the first three units, which took one of two forms: (1) Units 1–3 decreased sequentially in duration; or (2) Unit 2 was longest in duration (Fig. 6). No consistent interspecific patterns could be detected beyond the first three display units. Using this simple dichotomy, *A. conspersus* shares the temporal relationships of the first three units in its Type A display only with the southern and central (S&C) population of *A. grahami* (Type A) and with *A. garmani* (Type B; Fig. 6). However, *A. conspersus* and S&C *A. grahami* exhibit lengthy plateau-shaped first units with rapid acceleration/deceleration (Fig. 2b–c), whereas Unit 1 in *A. garmani* is lengthy because of an overall slower head rise and fall time (illustrated in Jenssen, 1981:fig. 1). In contrast, western *A. grahami*, *A. opalinus*, and the Type A display of *A. garmani* exhibit the temporal pattern where Unit 2 has the greatest duration.

*Display Evolution in Anolis conspersus.*—The presence of spiked headbob display unit mor-

phology in all Jamaican members of the *grahami* group aside from the S&C *A. grahami* population (Jenssen, 1979, 1981; this study) strongly suggests that the spike shape is the ancestral character state in the *grahami* group (Jenssen, 1981). Thus, the plateau-shaped Unit 1 in the Type A displays of S&C *A. grahami* and *A. conspersus* is shared either because of common ancestry (synapomorphy) or through independent derivation.

A recent mtDNA study of the *grahami* series anoles found that *A. conspersus* and the S&C population of *A. grahami* are approximately three times more closely related than S&C *A. grahami* is to *A. grahami* from western Jamaica (T. Jackman, D. J. Irschick, K. de Querioz, J. B. Losos, and A. Larson, unpubl.). This evidence strongly suggests that the plateau-shaped first unit of the Type A display has not evolved in parallel but instead is a shared, derived character.

Last, we would like to comment on the Type B display of *A. conspersus*. This display is unique within the *grahami* group, both in structure and in its consistent performance in relatively long volleys. If this display is autapomorphic in *A. conspersus*, then it has evolved within the past 2–3 million years. This proposition is based on the findings that Grand Cayman is not thought to have been continuously above water for much more than 2 million years ago (e.g., Haq et al., 1987; F. Burton, pers. comm.), and mtDNA sequence differences between *A. conspersus* and the S&C population of *A. grahami* correspond to an approximate divergence time of 2.8 million years ago (T. Jackman, D. J. Irschick, K. de Querioz, J. B. Losos, and A. Larson, unpubl.). Alternatively, if *A. grahami* diverged from *grahami* group stock prior to the splitting off of *A. opalinus* or *A. garmani*, then a homologue of the *A. conspersus* Type B display might be found outside the *grahami* group.

It is interesting to note that one species in the *lineatopus* group (*A. reconditus*) possesses a display that is similar enough in several respects to the Type B display of *A. conspersus* to make this speculation intriguing (Fig. 7). Thus, at present, we can conclude that the *A. conspersus* Type B display either is shared with one or more taxa outside the *grahami* group, or these display similarities have evolved independently. We currently are gathering the headbob display data on the remaining *grahami* series members required to test between these alternatives.

*Acknowledgments.*—We thank J. Losos, G. Gerber, and F. Burton for information about *A. conspersus* collecting locales and other field-related issues. D. Irschick (1993) and D. Veale (1997) assisted with the field collection of *A. conspersus*. Export of *A. conspersus* was authorized by A.

*Anolis conspersus*: 2nd peak after drop+pause  
*Anolis reconditus*: 2nd peak before drop+pause

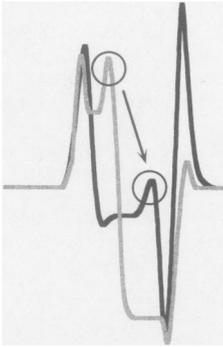


FIG. 7. Comparison of generalized headbob display unit structure for *Anolis conspersus* (black) and *Anolis reconditus* (gray) to illustrate similarities in form. (No axis is provided because actual time and amplitude scales differ.) The *A. conspersus* Type B display unit can be derived from that of *A. reconditus* by reducing the amplitude of the second peak (circled in gray) and pausing before rather than after its execution and by increasing the amplitude of the final up-sweep.

Benjamin, Chief Veterinary Officer, Department of Agriculture, Cayman Islands. We thank G. Ebanks Petrie, Department of the Environment, for permission to conduct this study, as well as J. Davies (1993), F. Burton, and P. Clifford (1997) for housing arrangements and hospitality. We are grateful to the Alma College undergraduates who contributed to this study by videotaping *A. conspersus* male contests and by gathering display coordinate data from those videotapes. Comments on earlier versions of this paper were provided by Y. Brandt, A. Echternacht, G. Gerber, D. Irschick, T. Jenssen, K. Orrell, G. Smith, and three anonymous reviewers. This research was supported by an Alma College Professional Development Award to DLC.

#### LITERATURE CITED

- BARLOW, G. W. 1968. Ethological units of behavior. In D. Ingle (ed.), *Central Nervous System and Fish Behaviour* pp. 217–232. Univ. of Chicago Press, Chicago.
- CARPENTER, C. C. 1962. Patterns of behavior in two Oklahoma lizards. *Am. Midl. Nat.* 67:132–151.
- CARPENTER, C. C., AND G. W. FERGUSON. 1977. Variation and evolution of stereotyped behavior in reptiles. In C. Ganz and D. W. Tinkle (eds.), *Biology of the Reptilia*. Vol. 7. Ecology and Behaviour A, pp. 335–554. Academic Press, New York.
- CASE, S. M. 1990. Dewlap and other variation in the lizards *Anolis distichus* and *A. brevirostris* (Reptilia: Iguanidae). *Biol. J. Linn. Soc.* 40:373–393.
- CHRISTMAN, S. P. 1980. Preliminary observations on the gray-throated form of *Anolis carolinensis* (Reptilia: Iguanidae). *Fla. Field Nat.* 8:11–16.
- COOPER, W. E., AND N. GREENBERG. 1992. Reptilian coloration and behavior. In C. Gans and D. Crews (eds.), *Biology of the Reptilia*. Vol. 18. Physiology E, Hormones, Brain and Behavior, pp. 298–422. Univ. of Chicago Press, Chicago.
- DECOURCY, K. R., AND T. A. JENSSEN. 1994. Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. *Anim. Behav.* 47:251–262.
- GRANT, C. 1940. The herpetology of the Cayman Islands. *Bull. Inst. Jamaica, Sci. Ser.* 2:1–65.
- FERGUSON, G. W. 1970. Variation and evolution of the pushup displays of the side-blotched lizard genus *Uta* (Iguanidae). *Syst. Zool.* 20:79–101.
- FLEISHMAN, L. J. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Am. Nat.* 139:S36–61.
- HAQ, B. U., J. HARDENBOL, AND P. R. VAIL. 1987. Chronology of fluctuating sea levels since the Triassic. *Science* 235:1156–1167.
- HASSON, O., R. HIBBARD, AND G. CEBALLOS. 1989. The pursuit deterrent function of tail-wagging in the zebra-tailed lizard (*Callisaurus draconoides*). *Can. J. Zool.* 67:1205–1209.
- HEDGES, S. B., AND K. L. BURNELL. 1990. The Jamaican radiation of *Anolis* (Sauria: Iguanidae): an analysis of relationships and biogeography using sequential electrophoresis. *Caribb. J. Sci.* 26:31–44.
- JENSSEN, T. A. 1971. Display analysis of *Anolis nebulosus*. *Copeia* 1971:197–209.
- . 1977. Evolution of anoline lizard display behavior. *Am. Zool.* 17:203–215.
- . 1978. Display diversity in anoline lizards and problems of interpretation. In N. Greenberg and P. D. Maclean (eds.), *Behavior and Neurology of Lizards: An Interdisciplinary Conference*, pp. 268–285. National Institutes of Mental Health, Rockville, MD.
- . 1979. Display behaviour of male *Anolis opalinus* (Sauria, Iguanidae): a case of weak display stereotypy. *Anim. Behav.* 27:173–184.
- . 1981. Unusual display behavior by *Anolis grahami* from western Jamaica. *Copeia* 1981:728–733.
- JENSSEN, T. A., AND N. L. GLADSON. 1984. A comparative display analysis of the *Anolis brevirostris* complex in Haiti. *J. Herpetol.* 18:217–230.
- JOLLIFFE, I. 1986. *Principle Components Analysis*. Springer-Verlag, New York.
- KLEINBAUM, D. G., AND L. L. KUPPER. 1978. *Applied Regression Analysis and Other Multivariate Methods*. Duxbury Press, Boston, MA.
- LEAL, M., AND J. A. RODRIGUEZ-ROBLES. 1997. Signalling displays during predator-prey interactions in a Puerto Rican anole, *Anolis cristatellus*. *Anim. Behav.* 54:1147–1154.
- LOVERN, M. B., T. A. JENSSEN, K. S. ORRELL, AND T. TUCHAK. 1998. Comparisons of temporal display structure across contexts and populations in male *Anolis carolinensis*: Signal stability or lability? *Herpetologica* 55:222–234.
- MACEDONIA, J. M. 1999. Color signal evolution in an ancestor-descendant species pair of Caribbean anoles. In J. Losos and M. Leal (eds.), *Anolis Newsletter V*, pp. 67–80 (available as a PDF file at: <http://>

- biosgi.wustl.edu/ lososlab/newsletter/newsletter.html).
- MACEDONIA, J. M., AND J. A. STAMPS. 1994. Species recognition in *Anolis grahami* (Sauria: Iguanidae): evidence from responses to video playbacks of conspecific and heterospecific displays. *Ethology* 98:246–264.
- MACEDONIA, J. M., S. JAMES, L. W. WITTLE, AND D. L. CLARK. 2000. Skin pigments and coloration in the Jamaican radiation of *Anolis* lizards. *J. Herpetol.* 34: 99–109.
- MARTINS, E. P., A. BISSELL, AND K. MORGAN. 1998. Population differences in a lizard communicative display: evidence for rapid change in structure and function. *Anim. Behav.* 56:1113–1119.
- MCKINNEY, C. O. 1971a. An analysis of zones of intergradation in the side-blotched lizard, *Uta stansburiana* (Sauria: Iguanidae). *Copeia* 1971:596–613.
- . 1971b. Individual and intrapopulation variation in the push-up display of *Uta stansburiana*. *Copeia* 1971:159–160.
- MINTON, S. A., AND M. R. MINTON. 1984. *Anolis sagrei*. *Herpetol. Rev.* 15:77.
- MORGAN, G. S. 1994. Late quaternary fossil vertebrates from the Cayman Islands. In M. A. Brunt and J. E. Davies (eds.), *The Cayman Islands: Natural History and Biogeography*, pp. 465–508. Kluwer Academic Press, Amsterdam, The Netherlands.
- WILLIAMS, E. E. 1976. West Indian anoles: A taxonomic and evolutionary summary. 1. Introduction and a species list. *Breviora* 440:1–21.
- Accepted: 28 August 2000.

*Journal of Herpetology*, Vol. 35, No. 2, pp. 310–315, 2001  
Copyright 2001 Society for the Study of Amphibians and Reptiles

## Adaptive Male Parental Care in the Giant Bullfrog, *Pyxicephalus adspersus*

C. L. COOK, J. W. H. FERGUSON,<sup>1</sup> AND S. R. TELFORD

*Department of Zoology and Entomology, Pretoria University, Pretoria, South Africa*

**ABSTRACT.**—Male giant bullfrogs *Pyxicephalus adspersus* exhibit paternal care through construction of channels that guide tadpoles to larger bodies of water. We found the following. These channels (which may exceed 15 m in length) make available cooler water to broods in the rapidly drying breeding puddles that frequently reach critically high temperatures. Eggs of *P. adspersus* exposed to temperatures above 38°C died, a temperature reached in a third of the puddles measured. In contrast, tadpoles readily survived temperatures above 38°C, and experiments showed that tadpoles can survive the highest temperatures recorded at the puddles. Males actively defended their offspring against predators and were sometimes killed while performing this behavior. Survival of eggs and larvae in territorial broods was roughly twice that of broods in nonterritorial breeding arenas. The large cost of paternal care in the giant bullfrog is therefore offset by strong fitness gains. We suggest that channel construction and predator defence, crucial for tadpole survival, can be performed most efficiently by large-bodied parents, explaining why males (not the smaller females) perform parental care.

Parental care has been reported in a number of frogs (Townsend, 1986; Summers, 1989; Kok et al., 1989), most of these from terrestrial breeders in the tropics (Wells, 1981). Either males or females can perform parental care. Paternal care is more likely in frogs than in other vertebrates because the cost of paternal care is usually low (Wells, 1981). This is exemplified in territorial species where eggs or tadpoles are deposited in a male's territory and where he cares for them while continuing to attract females (but see Townsend, 1986). Parental care may include

guarding of eggs or tadpoles against predation (Kluge, 1981), preventing desiccation (Townsend et al., 1984), maintaining access to water (Kok et al., 1989), and carrying tadpoles, either to water (Summers, 1990) or until development is completed (Wells, 1981).

Many anurans breed in ephemeral puddles (Wells, 1977; Sullivan, 1989). The hypothesized advantages of this habit is the absence of resident predators and reduction of competition for the tadpoles compared to those in permanent bodies of water (Wassersug, 1975), as well as a rapid rate of development (Heatwole et al., 1968; but for a counterargument, see Abe and Neto, 1991).

Giant bullfrogs, *Pyxicephalus adspersus* (adult

<sup>1</sup> Corresponding Author: E-mail: jwhferguson@zoology.up.ac.za.