DISPLAY REPERTOIRE OF A MALE *PHENACOSAURUS HETERODERMUS* (SAURIA: IGUANIDAE)

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ABSTRACT: The displays of a ♂ *Phenacosaurus heterodermus* (Sauria: Iguanidae) were recorded under social contexts of assertion, challenge, and courtship. Cinematographic analysis verified three very stereotyped display patterns, one more than the modal number reported for the display repertoires of non-anoline iguanid lizards. *Anolis* contains species which have expanded display repertoires, and the phenacosaurs appear to represent an early divergence from the Alpha Section of *Anolis*. Therefore, the three display types of *P. heterodermus* suggest that the phenomenon of expanded display repertoires was an early development in the behaviorial evolution of anoles. A method for quantifying head movement amplitude is presented.

DISPLAYS of lizards have been found to be stereotyped and species typical, or at least unique for populations (Blanc and Carpenter, 1969; Bussjaeger, 1971; Carpenter, 1961a, b, 1962a, b, 1963, 1965, 1966, 1967a; Carpenter and Grubitz, 1961; Carpenter et al., 1970; Clarke, 1965; Echelle et al., 1971a, b; Ferguson, 1971, 1973; Gorman, 1968; Jenssen, 1970, 1971; Kästle, 1963, 1965; Lynn, 1965; McKinney, 1971; Purdue and Carpenter, 1972a, b; Stamps, 1973).

The display repertoires of most iguanid lizards studied appear restricted to two distinct display patterns: the species unique "assertion-challenge" display pattern and a courtship display pattern which is quite similar within the family (see Bussjaeger, 1971:34–36 and Carpenter, 1967b:87–88). However, recent investigations have documented that within the genus *Anolis*, some species have a much larger and more flexible display repertoire than most iguanids (Hover, Jenssen, and Rothblum [unpubl. data]; Stamps and Barlow, 1973). Although thorough descriptive evidence is sparse, it is suspected this phenomenon of an expanded repertoire may be a common feature of anole behavior.

Of interest is whether the increased multiplicity of intraspecific display types occurred before, early, or late in the evolution of *Anolis*. This question can be initially approached by studying anoline species from selected species series and species of other genera having close phylogenetic affinities with *Anolis*.

The present study provides a qualitative and quantitative analysis of the *Phenacosaurus heterodermus* display repertoire. This species is closely allied with *Anolis*. Etheridge (1960) classifies *Phenacosaurus* as one of the "anole genera" along with *Chamaeleolis* and *Chamaelinorops*, and feels the phenacosaurs represent an early divergence from the primitive mainland stock of the *Anolis* Alpha Section.

MATERIALS AND METHODS

Dr. Ernest E. Williams collected specimens of *Phenacosaurus heterodermus* in August 1973 for taxonomic study, and temporarily housed some live individuals at the facilities of Dr. A. Stanley Rand, Smithsonian Tropical Research Institute, Canal Zone, where I had a brief opportunity to observe and film the species' behavior. The present report is based on the displays of a single male and is, therefore, not a definitive display description for the species. However, the observed displays were extremely stereotyped and provide significant data on a little known species.

Into a 1.2 m × 0.6 m × 0.7 m high photographic chamber fitted with potted plants, bromeliads, vines, and branches were placed two adult males and an adult female. One male was a brown morph collected just east of Tabio, Colombia. The other male and the female, both green morphs, were taken 8 km from the above locality, just south of Tenjo, Colombia.

The animals were observed within an 8-h

period. During this time, displays of the brown male were filmed with a super 8 camera, at a setting of ~~5–18 meters~~ =18 frames/second, and loaded with Kodachrome II® color film. Two 500-W floodlights with heat filters provided the light. One hundred thirty meters of film were exposed which included displays within assertion, challenge, and courtship social contexts as well as recording a complete courtship and copulation sequence.

Fourteen displays of the two major display patterns were selected from the filmed record which were complete, in focus, and of proper magnification and subject orientation to permit accurate analysis of head and dewlap movement. A frame-by-frame analysis was employed using a Kodak MFS-8 projector.

Besides temporal quantification of the display, this paper also provides quantification of head movement amplitude. To do this, a filmed display was selected in which the lizard was positioned with a near-perfect lateral orientation to the camera. I then took the following measurements: (1) distance from snout tip to middle of the eye, (2) head depth through the eye, (3) axilla-groin length, and (4) length of forearm from posterior margin of the elbow to deepest insertion of the phalanges. This display and its measured image then served as a standard for all subsequent filmed displays. Before a projected display was graphed, the length of one or more of the measured morphological features which were properly oriented in the film was matched to the standard by adjusting the distance between projector and graphing surface. In this way all displays of the filmed lizard were analyzed at approximately the same magnification. In addition to constant magnification, a second condition had to be satisfied. Only those filmed displays could be used in which head movement was in a vertical plane to the camera.

To evaluate stereotypy, the two major display types, A and B, were divided into artificially determined units. These units measured the durations for (1) head raising, (2) head lowering, and (3) periods when the head was held at a relatively constant level. Both display types A and B terminated with a series of rapid head oscillations. For these last movements the durations for head raising and lowering of each bob were lumped in the final presentation. Even with this condensation, a total of 21 units was necessitated in the A display and 27 units in the B display for accurate analysis. Descriptive statistics were run on the durations and amplitudes of each unit ($\bar{X} \pm$ SE), with 95% confidence limits of the means calculated for those units of adequate sample size.

Head movement amplitude was expressed in terms of the standard length described above for the tip of snout to mid-eye distance. The length of this designated standard appears at the bottom of each figure for reference purposes, and is also the unit measurement for the statistical descriptions of head movement amplitude. The 95% confidence limits for mean amplitudes were calculated only for the A display because of limited sample sizes of correctly oriented subjects in filmed sequences of the other display types.

RESULTS

A male *P. heterodermus* was found to have three quite distinct display types which were extremely stereotyped (Figs. 1 and 2).

A Display

The A display appeared in three contexts: (1) as the male secured a new perch site, but was not approaching another lizard nor directing his display at a conspecific; (2) used along with the B display type while displaying at another adult male; and (3) used with the C display type while displaying at a female and just preceding copulation with her. This display type is analogous to the "signature" display of *Anolis aeneus* (Stamps and Barlow, 1973).

The A display never involved dewlap ex-

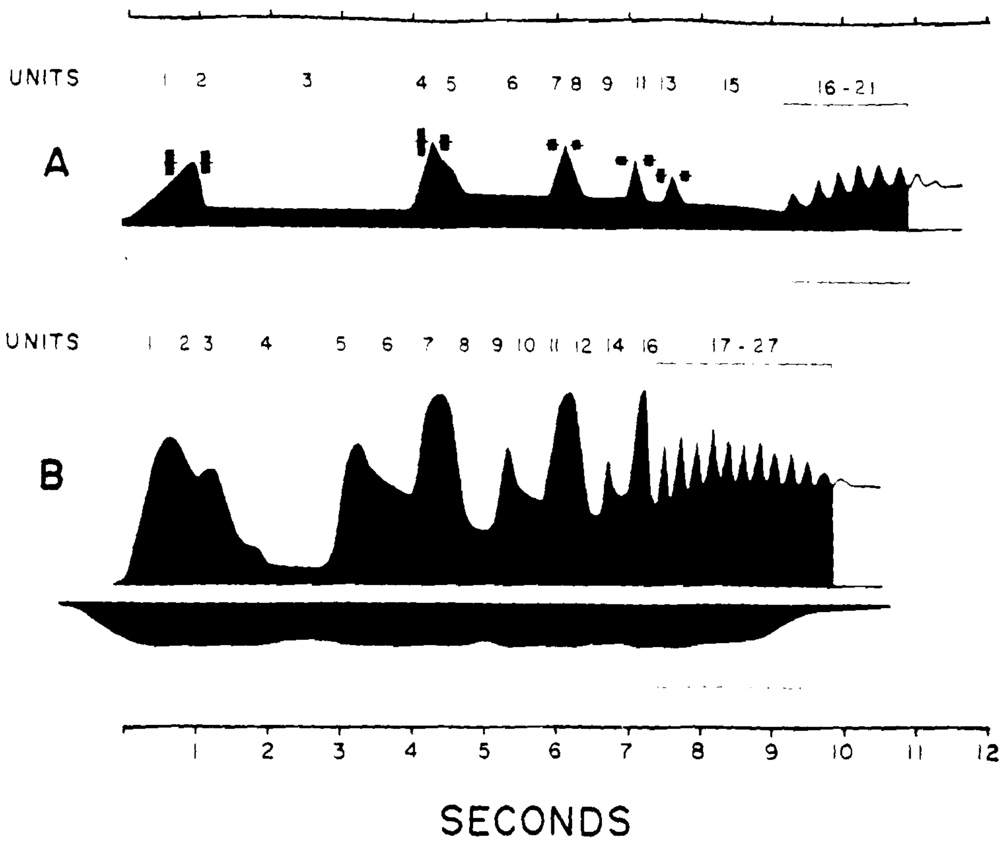

FIG. 1.—Display-action-pattern graphs of the A and B displays by a ♂ *Phenacosaurus heterodermus*. Unit durations and head movement amplitudes are mean values. Vertical black bars over the A display show 95% confidence limits for mean vertical movements of major head bobs. Black block below B display head movements represents dewlap extension. All figures are vertically scaled according to the snout tip to mid-eye length appearing in lower right corner.

tension, and was performed solely by movements of the head and neck. The lizard maintained his head at a near horizontal attitude throughout the vertical movements. This necessitated two pivot points, one at the head-neck junction and the other at the neck-shoulder articulation (Fig. 3a). The pattern consisted of five prominent head bobs intervened by four waiting periods (Fig. 1a). Durations of these motionless periods progressively decreased by approximately a factor of 0.4 (e.g. 2.8, 1.1, 0.6 and 0.2 s). After a fifth waiting period, the display terminated with six to seven rapid head bobs. Total elapsed time for the display was just under 11 s.

The durations for the display's 21 units showed very little variability (Table 1). No difference was found in the cadence even when comparing displays performed within different social contexts.

The head movement amplitude was not quite as stereotyped as display duration, but still had relatively narrow confidence limits (Fig. 1a and Table 2). Amplitude varied from subtle vertical movements while the male rested his head on a female's back just before and during intromission to more pro-

TABLE 1.—Mean ($\bar{x}$), standard error of the mean (SE), and 95% confidence limits of the mean (C.L.) for unit durations (expressed in seconds) of 11 A displays by a ♂ *Phenacosaurus heterodermus*.

Unit	$\bar{x}$	SE	Upper C.L.	Lower C.L.
1	0.93	0.05	1.03	0.88
2	0.20	0.01	0.22	0.17
3	2.78	0.03	2.85	2.71
4	0.33	0.01	0.36	0.31
5	0.17	0.01	0.51	0.46
6	1.13	0.01	1.16	1.10
7	0.21	0.01	0.23	0.19
8	0.27	0.01	0.28	0.26
9	0.57	0.01	0.59	0.54
10	0.14	0.01	0.16	0.12
11	0.16	0.01	0.18	0.14
12	0.21	0.01	0.23	0.19
13	0.12	0.01	0.13	0.11
14	0.17	0.01	0.18	0.15
15	0.38	0.03	1.44	1.33
16	0.36	0.01	0.39	0.34
17–21 (each unit)	0.27	0.00+	0.28	0.26

nounced amplitude while delivering an A display toward another male.

B Display

The B display was only seen directed at another male in an apparent challenge context. In this display type the dewlap was expanded, beginning its extension just before the head movements. Amplitude of the head movements was more than twice that in the A display (Figs. 1 and 3, Tables 2 and 3). The forelimbs as well as the neck were used to elevate the lizard's head during display. There was little tendency for the head to deviate from a straight alignment with the neck during vertical movement.

Though there were too few examples of the B display to calculate confidence limits, the variability of the unit durations and bob amplitudes was slight as evidenced by the small standard errors of the means (Table 3). As was true of the A display, the B pattern was very stereotyped.

The B pattern contained four double bobs. The first bob had a "big-little" amplitude sequence, while the next three double bobs were a "little-big" sequence. These last three bobs shared a common shape when graphed, except their durations progressively decreased by approximately a factor of 0.6 (e.g., 2.3, 1.4, and 0.8 s). This display terminated, as did the type A display, with a series of rapid head bobs. In the B display this series numbered 11–12

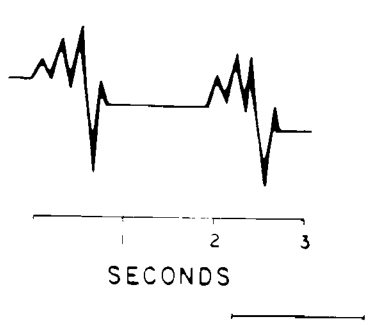

FIG. 2.—Display-action-pattern graph of two typical C displays performed in a volley by a ♂ *Phenacosaurus heterodermus*. Actual vertical head movements are scaled according to the snout tip to mid-eye length appearing in lower right corner.

TABLE 2.—Mean ($\bar{x}$), standard error of the mean (SE), and 95% confidence limits of the mean (C.L.) for those units having a change in head movement amplitude (expressed as the ratio: amplitude snout-mid eye length) for six A displays by a ♂ *Phenacosaurus heterodermus*.

Unit	$\bar{x}$	SE	Upper C.L.	Lower C.L.
1	0.54	0.05	0.67	0.41
2	0.45	0.05	0.57	0.33
4	0.68	0.05	0.81	0.56
5	0.52	0.03	0.60	0.44
7	0.53	0.02	0.57	0.49
8	0.53	0.01	0.56	0.50
10	0.37	0.01	0.40	0.33
11	0.41	0.02	0.47	0.36
13	0.26	0.03	0.33	0.20
14	0.27	0.02	0.32	0.22
16	0.17	0.02	0.23	0.12
17	0.26	0.01	0.29	0.23
18	0.26	0.01	0.29	0.23
19	0.27	0.01	0.30	0.24
20	0.24	0.01	0.27	0.21
21	0.19	0.02	0.24	0.15

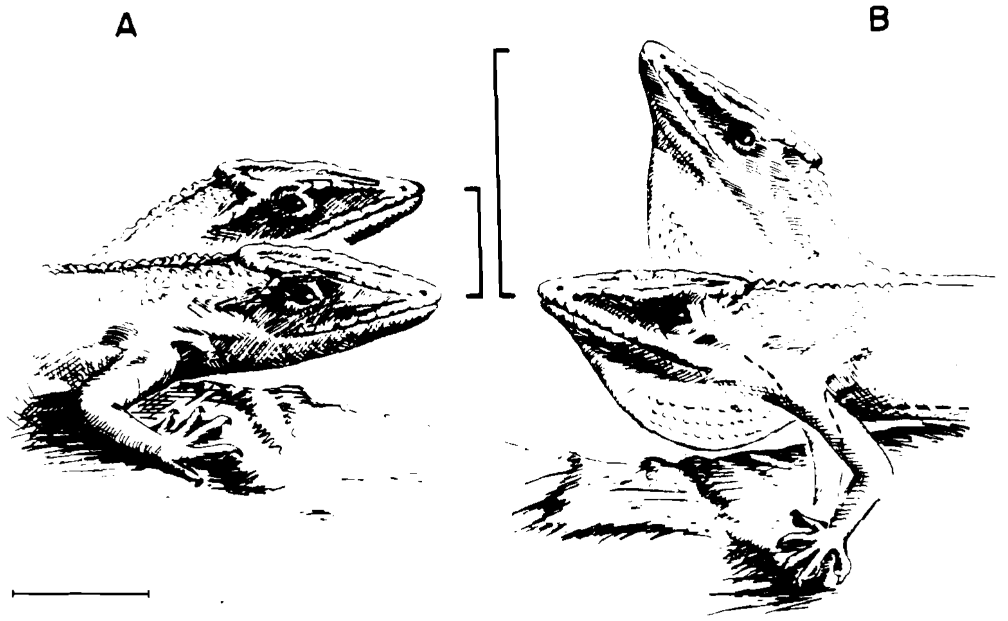

FIG. 3.—Maximum vertical head movements performed during A and B displays by a ♂ *Phenacosaurus heterodermus* are compared. Scale at lower left corner gives snout tip to mid-eye length.

bobs. Total duration of the B display was one second less than the A display.

The dewlap involvement was simply a protracted extension during the head movement. There was a slight suggestion that the fan might be pulsed to a limited extent. However, the movement of the throat fan was so subtle that it could well have been an artifact of the exaggerated head bobs, and probably not a relevant aspect of the display.

Discussion

Phenacosaurus heterodermus has three very stereotyped display types. The A display functions in several social contexts, including the assertion context, and serves as the signature display. The second pattern (B display) is a more vigorous behavior, is associated with male-to-male agonistic context, and serves as a challenge display. The last type (C display) is a brief series of rapid head bobs seen in the courtship context and has a pattern characteristic of courtship displays described for other species of Iguanidae.

P. heterodermus does not have a display repertoire the size of most non-*Anolis* iguanid lizards. From the review of Carpenter (1967b) and the extensive behavior study of the *spinosus* group of sceloporine lizards by Bussjaeger (1971), non-anoline iguanids have a simple repertoire of two display types. One is the rapid, low amplitude head nod display appearing only during courtship; a pattern reportedly shared by many iguanid species. The other type is a pattern unique for a species, or at least a population, which seems to declare territorial occupation or to maintain individual distance; it can be performed with or without a conspecific present. Under the latter condition, the pattern shows weak head movement amplitude with few or no accompanying modifiers (i.e., raised roach, side flattening, gorged throat). The display pattern produced under these low conflict or motivational situations has been called the "assertion" display. The same pattern performed under high conflict or motivating situations (i.e., male-to-male confrontations) contains exaggerated head movements with many concomitant modifiers and has been called the "challenge" display. To be stressed is that the behavior appearing in both categories involves the same pattern of head movements.

Functionally, this single "assertion-challenge" display type appears as two distinct display types in the repertoire of *P. heterodermus*. The A display was seen during all the contexts in which the non-anoline species are reported to give their assertion-challenge pattern, and the B display seems restricted to the challenge context. The use of an additional display type may indicate a greater communicative specificity for the various social situations encountered. Multiple display types within a species' behavioral repertoire is accentuated in *Anolis*. Based on studied anoles, there is a basic species typical pattern which Stamps and Barlow (1973) have named the "signature" display; it appears analogous to the assertion-challenge display type in other iguanid genera. However, beyond this display type some anoles have a *P. heterodermus* kind of repertoire in which there is an additional display type used almost exclusively in a challenge context (i.e., *Anolis nebulosus* [Jenssen, 1970]). Furthermore, other anoles use three or more display types in agonistic behavior (i.e., *Anolis townsendi* [Jenssen and Rothblum, unpubl. data], *Anolis limifrons* [Hover and Jenssen, unpubl. data], and *Anolis aeneus* [Stamps and Barlow, 1973]).

Etheridge (1960) considered *Phenacosaurus* to be an early branch on the *Anolis* phylogenetic tree; extant species of *Phenacosaurus* have very few external and osteological characteristics not found in the anoles (Lazell, 1969). Because phenacosaurs diverged early from *Anolis* and yet continue to show strong affinities with anoles, the expanded display repertoire of *P. heterodermus* suggests that the multiplicity of display types in *Anolis* species may have been a relatively old development in their behavioral evolution.

Table 3.—Mean ($\bar{x}$) and standard error of the mean (SE) for the unit durations (expressed in seconds) and unit head movement amplitude (expressed as the ratio: amplitude/snout-mid eye length) for three B displays by a ♂ *Phenacosaurus heterodermus*.

	Duration		Amplitude	
Unit	$\bar{x}$	SE	$\bar{x}$	SE
1	0.63	0.02	1.22	0.15
2	0.39	0.03	0.36	0.11
3	0.21	0.02	0.09	0.01
4	1.48	0.09	0.96	0.09
5	0.50	0.06	1.20	0.11
6	0.72	0.03	0.46	0.0[illegible]
7	0.39	0.00−	0.92	0.09
8	0.68	0.02	1.31	0.20
9	0.28	0.03	0.80	0.07
10	0.43	0.02	0.39	0.04
11	0.35	0.02	1.03	0.14
12	0.37	0.02	1.19	0.16
13	0.17	0.00+	0.49	0.08
14	0.20	0.02	0.32	0.07
15	0.28	0.00+	1.01	0.12
16	0.17	0.02	1.07	0.13
17–22 ($\bar{x}$ for each unit)	...	...	0.49	0.02
23–27 ($\bar{x}$ for each unit)	...	...	0.25	0.02
17–27 ($\bar{x}$ for each unit)	0.21	0.01	...	...
17–27 (total duration)	2.37	0.07	...	...

A second area to be discussed involves the report of Kästle (1965) on the display patterns of *Phenacosaurus richteri*. Lazell (1969) has recently made *P. richteri* a synonym of *P. heterodermus*; thus one would suspect our results would be similar. Also, the specimens with which Kästle worked were collected only about 20–25 km NE of where Williams captured the lizards on which I am reporting. Nevertheless, there are some discrepancies in display pattern and interpretation between our studies.

Kästle observed 49 displays of various types, but did not mention how many of these displays were filmed, what equipment he used, or how the films were analyzed. Study of the male displays under a challenge context was handicapped since he had only one male. All male-to-male related behavior was induced by models or a mirror.

The only display type on which we basically concur is his courtship display (Annäherungs or ANI) and my type C display.

Kästle's species recognition behavior (Arterkennungs-Imponieren or AEI) seems a mixture of my A and B type displays. The display-action-pattern graph presented in his Fig. 4 shows two patterns, one without dewlap extension, and one with an extended dewlap; the former bears no resemblance to my A display, while the latter is roughly similar to my type B display. Kästle (1965: 755) also says the AEI displays could increase in total number and frequency of head bobs as well as having no fixed rhythm. In light of the extreme stereotypy I found in *P. heterodermus* displays in dewlap usage, cadence, and pattern, there is a high probability Kästle lumped what I found to be the A and B display types.

His challenge behavior (Droh-Imponieren) encompassed a broad spectrum of behavior in which are included many modifiers such as rolling up of the tail, flattening of body sides, and opened mouth (Kästle, 1965:758–9). He emphasized the anterior-posterior swaying (Schwanken) of his male and seemed to present this movement as the major element of the challenge display pattern. Kästle reported this swaying was at times followed by head nodding in a manner of an AEI display. Kästle's Fig. 8 shows a pattern of swaying listed under his challenge behavior which is very similar to his AEI display graphed in Fig. 4b; both of these patterns somewhat resemble my B display.

To resolve the discrepancies between our findings, I offer the following conjecture. I believe Kästle did not adequately define the type A display which is presumably represented in his Fig. 4a (though this display pattern could very likely vary between populations), and included some of the type B challenge displays in the less appropriate AEI category (the pattern in his Fig. 4b). Both of these bob patterns he considers as one display type. Other more intensely performed B displays were probably preceded or accompanied by prominent swaying movement which he seemed to use as a criterion for challenge displays. The swaying, however, is most likely a dynamic modifier associated with the B display when the animal becomes increasingly excited. Male *A. nebulosus* can perform accentuated swaying behavior preceding their challenge display when displaying before a mirror (pers. observ.).

The body postures and swaying movements Kästle described as challenge behavior are missing from my report. I believe these were simply not expressed during my brief period of observation because the interacting males were never strongly aroused; the brown morph's dominance was not contested by the other male.

A last point which may be responsible for our differing results may involve our approaches. I have isolated distinct head nodding patterns, called each a distinct display type, and then listed the social contexts in which each appeared. Kästle seemed to have named his display types according to social context and then listed the various behaviors which appeared within each context.

Considering the potential for taxonomic and systematic application of saurian displays, a quantitative approach cannot be overemphasized. Furthermore, when working with species having a large display repertoire, the social function of each display type must be ascertained before the display pattern can be properly compared with other species. Therefore, because of the limited data on which the present study and Kästle's (1965) work are based, the details of *P. heterodermus* (= *P. richteri*) display behavior should be viewed as preliminary until greater numbers of this species are surveyed.

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