Herpetologica, 35(1), 1979, 21–30

DISPLAY MODIFIERS OF *ANOLIS OPALINUS* (LACERTILIA: IGUANIDAE)

THOMAS A. JENSSEN

ABSTRACT: The Jamaican lizard *Anolis opalinus* has 7 static modifiers (optional body postures) and 6 dynamic modifiers (optional display movements) that can appear with the head-bobbing display. The modifiers probably have a much more important communicative function in *A. opalinus* than in most anoles, because *A. opalinus* demonstrates little predictability in its head-bob display *per se*.

Static modifiers alter the appearance of the displayer. They are added to the head-bob displays during agonistic interactions. These modifiers are combined progressively and seem to indicate the relative arousal of the displayer.

Dynamic modifiers alter the appearance of the display. Their contribution to the message content of the display may be broader than that of static modifiers because they are used in more contexts. Some dynamic modifiers are restricted to male-male contexts, whereas others appear in several contexts. These movements can also be performed independently of the head-bob display.

Key words: *Anolis*; Behavior; Jamaica; Lacertilia

THE display behavior of *Anolis opalinus* is unusual for an iguanid lizard because the species does not have a single distinctly stereotyped head-bobbing pattern in its display repertoire (Jenssen, 1979). During social interactions, the most predictable aspect of display behavior of this species is the use of display modifiers. Display modifiers are optional postures and movements with which most iguanid lizards elaborate their stereotyped head-bob displays. The kinds and numbers of modifiers added to a head-bob display seem to indicate relative arousal of the performer (Jenssen, 1977, 1978; Jenssen and Hover, 1976). For *A. opalinus* the display modifiers appear to have a more important communication function than the species' head-bobbing display.

MATERIALS AND METHODS

This analysis of display modifiers is based on display behaviors observed and filmed in the field. Extended field observations were made in Mandeville, Jamaica, from March 1970 to March 1971 and during the summers of 1971 and 1975. Data were gathered from populations of marked lizards as they interacted under natural conditions. Observations were aided by binoculars, and verbal descriptions of the behavior were recorded on tape.

The filmed record of *A. opalinus* behavior was composed of 639 displays performed by 51 males. Of these, 196 displays were filmed in the field and 443 came from captive animals placed in a 1.3 × 0.7 × 0.4 m enclosure in my Jamaican residence.

The films were analyzed frame-by-frame as described by Jenssen and Hover (1976). Sixteen variables were recorded from each display analyzed (e.g., number and kinds of modifiers/display, social context of the display, number of bobs/display, bob-cadence/display, number of dewlap-pulses/display). Because stereotyped head-bobbing behavior was not evident, the data were examined with an involved computer-assisted methodology. These methods and results of the analysis of head-bob display are detailed elsewhere (Jenssen, 1979).

The present methods provide an ethogram of the modifiers which accompany head-bob displays of *A. opalinus* and correlate the occurrence of the modifiers with social context. The contexts were of four kinds: nondirected or male alone, male-

female, male-male, and male-congener. The social function of each modifier was inferred from the context in which the lizard used it.

Results and Discussion

Just as animal communication can be characterized by a variety of criteria (Burghardt, 1970), the term "display" is also subject to more than one definition (e.g., Brown, 1975: 275–277; Heymer, 1977: 91; Wilson, 1975: 582). For the present paper, I am restricting definition of lizard display to a narrow class of behavior: stereotyped, species-typical head and/or dewlap movements.

In studying head-bob displays of anoline lizards, the first step is to establish the syntactics of the displays. This involves differentiating between display elements which are present during all performances of a particular display pattern (i.e., elements comprising the core display) and those elements which are not always associated with each performance of a particular display pattern (i.e., elements which are display modifiers). The latter are optional elements I label as static modifiers if they are postures and dynamic modifiers if they are movements (see Jenssen, 1977, 1978).

Static modifiers change the appearance of the displayer, and dynamic modifiers alter the appearance of the display. To be considered a display modifier, a posture must occur concurrent with the head-bob display, and a movement must be either concurrent with the head-bob display or attached to the beginning or end of the core display.

For *A. opalinus*, the core display is elusive and at best is represented by an abstract theme. As documented elsewhere (Jenssen, 1979), the head-bob display of *A. opalinus* consists of 4–11 bobs followed by 0–8 dewlap pulses. The bob patterns for most of the displays were explained by the following theme: (1) an initial series of two bobs, (2) a middle series of bobs in which the cadence of bobs progressively quickens, and (3) a concluding series of bobs in which the cadence progressively slows. With the exception of this theme, the head-bob behavior of *A. opalinus* lacked a stereotyped core display and was unpredictable; few of the measured display variables covaried (Jenssen, 1979). The display modifiers, on the other hand, represent a much more ordered system than the head-bob displays *per se*.

Static Modifiers

Two generalizations appeared. First, static modifiers are used primarily during agonistic situations, usually male-male encounters, although at times males employ static modifiers during courtship when the male is small and the female seems unreceptive.

Second, there is an additive hierarchy of static modifiers in *A. opalinus* that seems to indicate increasing arousal. Thus, static modifiers are not randomly employed; rather there is a progression of specific modifiers which are added together as interactions become prolonged. The first static modifiers to appear are also those most frequently used, such as erected dorsal crest or lowered hyoid apparatus (see below). If interacting males retreat after their initial contact or if dominance is quickly established, then no additional modifiers are added to erected crest or gorged throat in succeeding head-bob displays. If the interaction persists, however, then more modifiers appear with subsequent displays as the males escalate their encounter.

The frequency with which static modifiers occur reflects their hierarchal usage. The static modifiers listed below for *A. opalinus* are ordered by frequency of occurrence, from the most common to the least common.

Erected crest.—The erectible crest is restricted to the neck region. Usually crest erection is subtle, but in rare instances of extended agonistic interactions it becomes prominent. This modifier appeared in 48% of the recorded displays. Although pri-

marily associated with male-male encounters, erect crest was seen in 13% of the male-female interactions, particularly when the male was smaller than average (<47 mm SVL). The appearance of this modifier has a short lag period after the initial conspecific contact and persists after the conclusion of the contact; it may possibly be under adrenergic control and thus be an indicator of increased sympathetic nervous activity. This modifier has been reported in every behavioral study of anoline lizards.

Gorged throat.—This modifier is effected when the lizard lowers its hyoid apparatus, giving the throat a swollen appearance. Gorged throat appeared in 34% of all displays and frequently was the first modifier seen. This was true when two males encountered each other unexpectedly at close range, as happened in enclosures. If males approach each other from a distance, the erected crest usually precedes gorged throat. Unlike the raised crest, a lowered hyoid apparatus is not necessarily held throughout an encounter or volley of displays. This static modifier is also characteristic of other species of *Anolis*.

Orbed eyes.—This modifier consists of dilation of the pupils and of widely opened eyelids. The effect is rounded eyes of larger than normal dimensions. During elaborate aggressive display (e.g., displays with cocked head), the orbital area looks slightly distended and the eyes are slightly bulged. The dilated pupils presumably reflect increased activity of the sympathetic nervous system.

Orbed eyes were recorded with 11% of the displays. However, because it is a graded response, subtle expression of this modifier probably went undetected, particularly if camera angle or image size was not optimal for viewing the lizard's eye.

Although it is mentioned infrequently in the literature on anoline displays, I suspect that orbed eyes is a response in an aroused lizard common to all species of *Anolis*.

Opened mouth.—The mouth is held partially opened. Although the extent is variable, the mouth is never widely gaped. This posture appeared in 15% of the sample, mainly in male-male encounters. There were three displays during which this modifier was used by a small male while courting an aggressive female.

An opened mouth during display is common in anolines and seems to be an intention behavior to bite; it is used by disputing animals when they are at close range.

Protruded tongue.—During this posture part of the tongue is held out beyond the lips (see Figs. 1, 3). Tongue protrusion occurred in 9% of the recorded displays. With the exception of one thwarted courtship attempt, this modifier was only seen during male-male interactions.

Protruded tongue is not found in all *Anolis* (e.g., *Anolis nebulosus*; Jenssen, 1970, 1971). However, it has been reported to accompany the displays of *Anolis carpenteri* (Echelle et al., 1971*b*), *Anolis evermanni* (Ruibal, 1967), *Anolis gundlachi* (Ruibal, 1967), *Anolis limifrons* (Echelle et al., 1971*a*; Hover and Jenssen, 1976; Jenssen and Hover, 1976), *Anolis lineatopus* (Rand, 1967; Ruibal, 1967), *Anolis lucius* (Ruibal, 1967), and *Anolis townsendi* (Jenssen and Rothblum, 1977).

Cocked head.—This is a peculiar posture which, when fully expressed, results in the head being cocked almost 90° to the longitudinal body axis, the snout pointing downward, the neck becoming the highest point on the body, and the center of gravity of the body shifting over the fore- and hindlimbs away from the side to which the head is cocked (Fig. 1). While facing his adversary from a normal stance, the male quickly (≈0.3–0.4 s) assumes the cocked-head posture. This is accomplished by straightening the rear limbs, thus partially elevating the pelvic region and pushing the body forward; at the same time the forelimbs are extended vertically, and the body weight is shifted over the outside arm. This posture is always accompanied by other static modifiers. The cocked head is assumed at the beginning of the head-bob display and can be held throughout the entire head-bobbing sequence. Cocked head occurred in 3% of

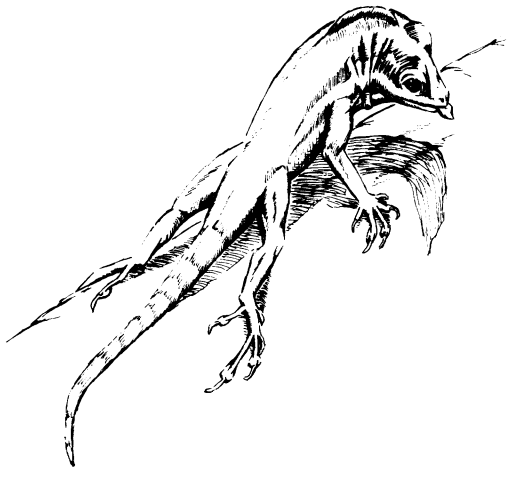

FIG. 1.—Male *Anolis opalinus* in a head-cock posture.

the recorded displays, and was associated with male-male interactions.

Field notes indicate that neighboring males involved in territorial interactions frequently use head-cock without display (Table 1). This posture may be held for as long as 30–45 s. The prolonged head-cock is performed at the edge of the male's territory and he does not approach his neighbor beyond this point. Head-cocking may indicate to an adversary where the posturing male will make a territorial defense.

Lateral compression.—Lateral compression of the body is a static modifier common in iguanid species, including *A. opalinus*. However, because *A. opalinus* is stout bodied, lateral compression was difficult to assess from the filmed displays and was not analyzed.

Dynamic Modifiers

As a group, dynamic modifiers are not used in a progressive fashion because they do not all appear in the same social context. Some dynamic modifiers are obviously aggressive signals, whereas others appear in

TABLE 1.—Frequency of occurrence of head-bobbing displays by males and of other movements that may be associated with, or independent of, the head-bobbing display. Data were collected in Mandeville, Jamaica, during 16.5 h of observing a field population of marked *Anolis opalinus* in February 1971.

	Social context			
Behavior	♂ alone	♂:♀	♂:♂	Interspecific
Head-bobbing display	38	71	48	15
Circumduction				
With display	----	----	1 (2%)	----
Without display	----	----	5	4
Rearing				
With display	----	----	20 (42%)	----
Without display	----	----	----	----
Head-roll (exaggerated)				
With display	----	----	4 (8%)	----
Without display	----	----	6	----
Dewlap pulsing				
With display (prior pulse)	2 (5%)	5 (7%)	4 (8%)	3 (20%)
Without display	104	31	34	10
Step-bobbing				
With display	7 (18%)	5 (7%)	6 (13%)	9 (60%)
Without display	10	2	6	1
Rapid head-bobs				
With display	----	8 (11%)	1 (2%)	----
Without display	----	10	3	----

FIG. 2.—Forelimb movement by male *Anolis opalinus* when circumducting.

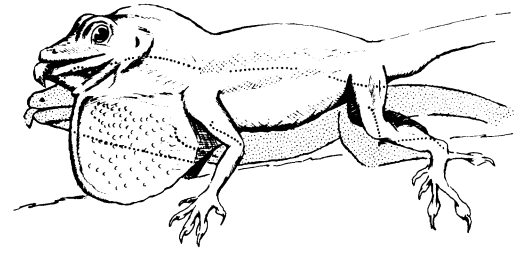

FIG. 3.—Amplitude shift (beginning with shaded position) of male *Anolis opalinus* when rearing.

several contexts and have less evident functions (Table 1). The dynamic modifiers are also performed independently of the display behavior (Table 1).

Circumduction.—A stationary lizard performs this modifier just before its display by lifting a forefoot, with toes curled upward, and circumscribing an arc in the air. The foot travels simultaneously backward, upward, and slightly out from the body; then it arcs forward and down to stop at about its initial position on the substrate (Fig. 2). The duration is variable (0.4–1.0 s), and the expression is graded, from the foot being barely raised to the performance of an arc peaking almost at shoulder height. A very similar behavior has been described for several agamid lizards of the genus *Amphibolurus* (Carpenter et al., 1970), in which it seems to be a submissive gesture. In *A. opalinus*, however, circumduction appears to be agonistic.

This behavior was only seen during 2% of the male-male displays and appeared in interspecific interactions (Table 1); it prefaced displays accompanied by other modifiers. The forelimb closest to the displayer's adversary was always the circumducted leg.

I believe circumduction is an intention movement ritualizing an approach toward an antagonist. Circumduction is like walking in place. Evidence for this interpretation comes from observations of interacting males where one is approaching the other. On occasion the moving male will exaggerate the walking movements of one of his forelimbs such that the forward return of the foot goes through a pronounced arc.

Rearing.—Rearing consists of hindlimb extension during dewlap extension. The forelimbs are already extended to allow for the expanding dewlap, so rearing results in a four-legged stance with the tail weakly arched (Fig. 3). The elevated pelvis is then lowered as the dewlap retracts.

Rearing can occur (1) with the dewlap pulses following bobbing and (2) with pulsing which may appear before head-bobbing (see below). In the former situation, rearing may be performed with each subsequent pulse; however, hindlimb amplitude decreases with successive pulses.

Rearing appears to elaborate pulses of the display. Rearing is graded in expression, varying from subtle hindlimb input to full extension of the hindlimbs accompanied by a backward movement of the entire body. This modifier occurred infrequently in the laboratory (3% of the displays), but modified 42% of the head-bob displays given in agonistic contexts in the field (Table 1). It was only seen in male-male encounters and was accompanied by static modifiers.

Head-roll.—This is simply a raising and lowering of the head just before the lizard begins its head-bob display. In this introductory movement, the head is at a higher amplitude at the conclusion of the roll than at the start (Fig. 4a). The actual amplitude of the head-roll is quite variable and at times is accompanied by a prior-pulse movement.

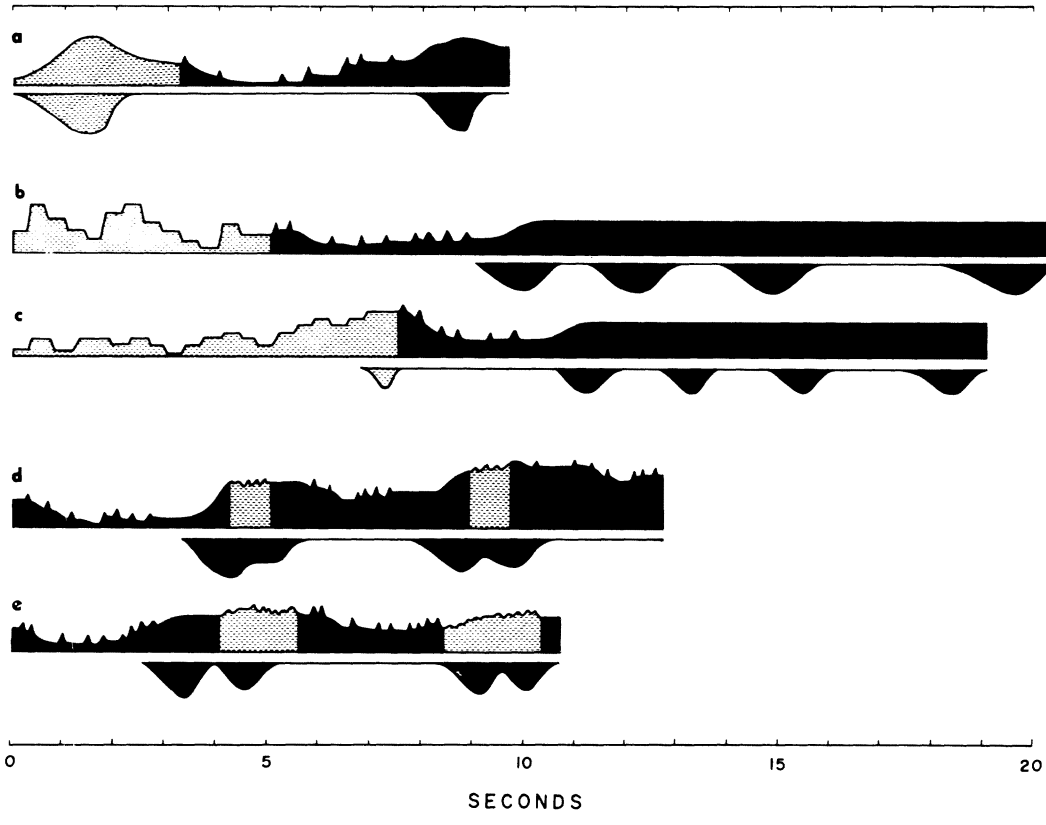

FIG. 4.—Graphs of display-action-pattern of *Anolis opalinus* displays. Solid dark areas indicate the head-bob portion of the displays, and shaded areas indicate the dynamic modifiers: prior pulse (a), head roll (a), step-bobbing (b and c), and rapid head-bobs (d and e). Upper block of each figure shows head amplitude and lower block shows dewlap extension through time.

Introductory head-rolls are also reported in the displays of *A. townsendi* (Jenssen and Rothblum, 1977), *A. aeneus* (Stamps and Barlow, 1973), and *A. limifrons* (Jenssen and Hover, 1976). They are probably a common dynamic modifier in many anoline species.

Prior-pulse.—This is a pulsing of the dewlap which occurs as an optional introduction to the head-bob display. Usually a prior-pulse is concluded just before bobbing begins (Fig. 4a), but on occasion the dewlap is not completely retracted before bobbing is initiated. This modifier is also graded from a partial extension of the dewlap with no head roll to full dewlap extension, an exaggerated head-roll, and rearing. Head-bob displays with prior-pulses are performed in all four contexts (Table 1).

Optional dewlap pulses immediately preceding the stereotyped display are performed by *A. townsendi* (Jenssen and Rothblum, 1977) and *A. aeneus* (Stamps and Barlow, 1973). Like the head-roll modifier, prior-pulse is probably employed by many species of *Anolis*.

Step-bobbing.—This introductory movement consists of quick upward and downward movements of the body or of just the head, interspersed with short "plateaus" (body motionless through time); when change in amplitude is plotted against time, the behavior produces a step-like graph. The duration and pattern of the movements

are most unpredictable (Fig. 4b,c). Step-bobs can also be accompanied by dewlap pulses at any time during their performance.

Step-bobbing can be effected with the neck alone, with forelimb input, or infrequently with all four limbs. It is performed with displays having no other modifiers, as well as with displays having many modifiers (e.g., erected crest, gorged throat, tongue out, and rearing). In addition, displays with step-bobbing were seen in many contexts (e.g., with no other lizard about, directed at a distant male or female, directed at a male during close-quarter displaying and directed at congeners) (Table 1). I have no idea what function step-bobbing serves.

Of importance to ethologists is the fact that step-bobbing was commonly seen in the field, but was never performed by captive animals. This is a case where field observations were necessary to augment behavior studied under laboratory conditions.

Rand (1967) observed an analogous behavior in the Jamaican *A. lineatopus* that he called "step bobbing." I have followed his terminology. Stamps and Barlow (1973) described an analogous behavior for *A. aeneus* that they called a "jerkbob." This dynamic modifier is not common to most anoline species.

Rapid head-bobs.—This behavior is a series of shallow, rapid head-bobs of extremely variable number (Fig. 4d,e). Rapid head-bobs are usually separated temporally from the head-bobbing display; however, for those displays where rapid head-bobs serve as a modifier, they occur just before the display (even during a prior-pulse), during the dewlap pulsing of the display, or after the display. Most often, rapid head-bobs are directed at a female during courtship (11% of female-directed displays; Table 1). Although not in the data of Table 1, solitary males were also seen performing displays with this modifier just before they changed their perch sites (non-directed or assertion context) and during male-male interactions. This modifier was not seen with displays having more than an erected crest and increased limb amplitude as modifiers.

Rapid head-bobs have been observed in almost all iguanid lizards studied and have been given numerous labels (e.g., jiggling, courtship nods, shuddering, multibobs). They have been associated with courtship (Jenssen, 1977); however, there is now some doubt that rapid head-bobbing is exclusively a courtship signal (Rothblum and Jenssen, 1978; Ruby, 1977; Stamps and Barlow, 1973).

Limb amplitude.—The vertical head-bobbing movements of *A. opalinus* can be produced by the neck muscles, or there can be added amplitude contributed by forelimb or by forelimb and hindlimb extension; the increased amplitude can be considered a dynamic modifier. From the analysis of 639 displays, it was found that (1) 52% of the displays were effected by neck movement with little or no forelimb input, (2) 40% had obvious forelimb extension with little or no hindlimb input, and (3) 8% were performed with the body lifted from the substrate by extension of forelimbs and hindlimbs.

Head-bob displays having increased limb amplitude tended also to have more static modifiers. The displays were placed into the above three groups according to their relative amplitude; there were significant differences in the frequency distributions of the number of static modifiers when comparing the three limb amplitude groups (chi-square test for k independent samples $= \chi^2 = 222.4$, df $= 12$, $P < 0.001$; Siegel, 1956). The mean number of modifiers appearing with low amplitude displays, 2-leg pushup displays, and 4-leg pushup displays were 1.2, 2.1, and 3.1, respectively (Fig. 5). Displays executed with 2-leg pushups and 4-leg pushups tend to occur when the males are aroused by significant social contact (e.g., prolonged courting, display exchanges by adjacent territorial males, interactions between intruding and resident males), but are not associated

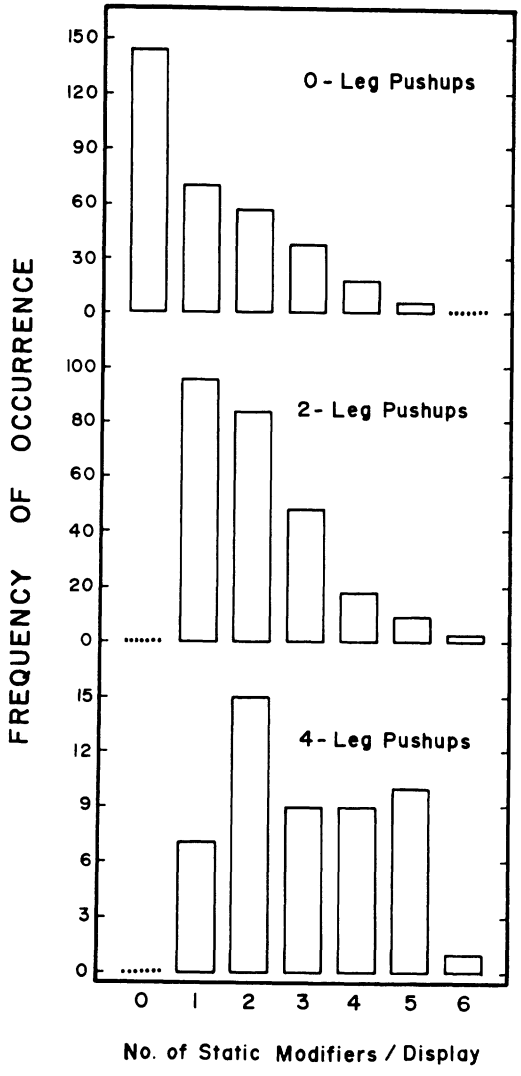

FIG. 5.—Frequency distributions of the number of modifiers accompanying 639 displays of *Anolis opalinus* when grouped according to relative limb amplitude during the head-bobbing display.

solely with aggressive contexts. The ability of an individual to alter the amplitude between its displays is a dynamic modifier common to many anoline lizards.

Agonistic Interactions

To demonstrate how the displays and modifiers are used during aggressive contact, I offer the following anecdote (Collins study area, Mandeville, 2 February 1971).

Male 3 (53 mm SVL, 2.92 g body wt) and male 9 (51 mm SVL, 2.75 g body wt) were disputing in the rafters of an old shed, part of which was included in the territory of both lizards.

11:25 Male 3 is on wall under rafter 6 (slightly into ♂ 9 territory) eating ants. Male 9 is on rafter 6 watching ♂ 3 from a distance of 1.5 m. Male 3 eats an ant and pulses its dewlap once without head-bobs. Male 9 moves 0.5 m toward ♂ 3.

11:26 Male 3 moves to top of wall. No display. Male 9 advances quickly two body lengths, then another body length (crest slightly erect). Male 3 watches. Male 9 gorges its throat as ♂ 3 slowly climbs to rafter 6 (males 0.6 m apart).

11:27 Male 3 head-cocks (holds posture 9 s), then straightens body, and they stare at each other. Now crest slightly erect on ♂ 3.

11:29 Male 3 head-cocks (12 s) again with gorged throat and crest erect. Then he advances one body length and head-cocks (5 s).

11:30 Male 3 head-cocks (10 s) and retreats slowly on cross brace toward his own territory.

11:33 Male 3 head-cocks (7 s) then gives three consecutive head-rolls. Male 9 immediately head-cocks (45 s) and moves toward ♂ 3. Males are 0.5 m apart.

11:35 Male 9 gives several head-rolls attached to a D_{8b3p} (display with 8 bobs and 3 pulses). Male 3 then circumducts and gives a D_{7b1p} (rears on 1st pulse), D_{6b1p} (rears on 1st pulse), and a D_{7b7p} (rears on 1st pulse to the extent he goes backwards several steps).

11:38 After about 3 min of staring at each other, ♂ 3 circumducts and gives three deep head-rolls introducing a D_{5b1p} (with rearing), followed by a D_{8b4p} (with rearing on 1st pulse).

11:39 Male 9 gives a prior-pulse D_{7b5p} and ♂ 3 head-cocks (30 s). Then they stare at each other.

11:41 Male 9 head-cocks (35 s), moves half a body length toward ♂ 3 and head-cocks (11 s), and then circumducts twice followed by a D_{8b1p} (rearing back 3 paces), D_{7b1p} (rearing), and a D_{7b3p}. Male 3 watches with gorged throat and erect crest.

11:43 Male 9 advances to within one body length of ♂ 3. They both exchange D_{6b0p} with erected crests, gorged throats, and orbed eyes. Then they begin to jaw-spar. (In jaw-sparring, two males are faced off head-to-head, with mouths usually partially open. One male will begin by swinging his head into contact with the side of the head of the other male in almost a slapping movement. Upon contact the second male pushes off on the first male's head in a countering move

(Fig. 6). They are in position to bite the other's neck or forelimb, but continue to parry each other's stereotyped attempts at a hold on the jaw. Jaw-sparring can culminate in locked jaws.) During the jaw-sparring, the males made short, but very audible, squeaking sounds.

11:44 Male 9 then backed off one body length. After a minute of staring, ♂ 3 initiated another exchange of head-bobbing displays without pulses and moved in to resume jaw-sparring. The encounter ended with ♂ 9 backing off into his territory.

Overview

For most anoles the head-bobbing displays appear central to the communication system. Each species has a repertoire of one or more stereotyped bob patterns which is a basis for such probable functions as species recognition and mate selection (Jenssen, 1977). The species indicate relative arousal by adding optional components to this stereotyped core behavior. For instance, as *Anolis limifrons* becomes more aroused, it adds more head-bobs to its signature display (Jenssen and Hover, 1976); or during extended male-male encounters, it escalates the interaction by progressively using five different display patterns (Hover and Jenssen, 1976). However, *A. opalinus* has no distinctly stereotyped bob pattern nor could I find any display variable correlated with context or intra-display events (Jenssen, 1979).

Therefore, the postures and movements serving as the static and dynamic modifiers appear to be more important in the social communication of *A. opalinus* than head-bobbing behavior. The above anecdote provides an excellent narrative of how the non-bobbing behavior is used extensively and many times independently of the head-bobbing displays in social interactions of *A. opalinus*. When performed as modifiers to the species' head-bob display, the progressive addition of postures appears to provide an index to the relative arousal of the displayer, and many of the dynamic modifiers, as suggested by their use (Table 1), seem to give the head-bobbing display a different message content.

FIG. 6.—Jaw-sparring between two male *Anolis opalinus* showing first the head thrusts of one male and then those of the other. Shaded areas give starting positions.

Acknowledgments.—Francis and Shirley Collins extended their friendship and access to their Mandeville property, for which I am most grateful. Aspects of this study were supported by NIMH (postdoctoral fellowship GF02M4 33435-01A1) and NSF (BMS 74-20143 to T. A. Jenssen and B 019801X to E. E. Williams). I am indebted to Risa Jenssen and Pam Hollandsworth, who critiqued and typed the manuscript, respectively.

LITERATURE CITED

BROWN, J. L. 1975. The Evolution of Behavior. W. W. Norton, New York.

BURGHARDT, G. M. 1970. Defining "communication." Pp. 5–18 *in* Johnston, J., D. Moulton, and A. Turk (Eds.), Communication by Chemical Signals. Vol. I. Meredith Corp., New York.

CARPENTER, C. C., J. A. BADHAM, AND B. KIMBLE. 1970. Behavior patterns of three species of *Amphibolurus* (Agamidae). Copeia 1970:497–505.

ECHELLE, A. A., A. F. ECHELLE, AND H. S. FITCH. 1971*a*. A comparative analysis of aggressive display in nine species of Costa Rican *Anolis*. Herpetologica 27:271–288.

———. 1971*b*. A new anole from Costa Rica. Herpetologica 27:354–362.

HEYMER, A. 1977. Ethological Dictionary. Verlag Paul Parey, Berlin and Hamburg.

HOVER, E. L., AND T. A. JENSSEN. 1976. Descriptive analysis and social correlates of agonistic displays of *Anolis limifrons* (Sauria, Iguanidae). Behaviour 58:173–191.

JENSSEN, T. A. 1970. The ethoecology of *Anoli*

nebulosus (Sauria, Iguanidae). J. Herpetol. 4: 1–38.

———. 1971. Display analysis of *Anolis nebulosus* (Sauria, Iguanidae). Copeia 1971:197–209.

———. 1977. Evolution of anoline lizard display behavior. Am. Zool. 17:203–215.

———. 1978. Display diversity of anoline lizards and problems of interpretation. Pp. 269–285 *in* Greenberg, N., and P. MacLean (Eds.), Behavior and Neurology of Lizards: An Interdisciplinary Conference. N.I.M.H., Rockville, MD.

———. 1979. Display behaviour of male Anolis *opalinus* (Sauria, Iguanidae): A case of weak display stereotypy. Anim. Behav. 27:173–184.

JENSSEN, T. A., AND E. L. HOVER. 1976. Display analysis of the signature display of *Anolis limifrons* (Sauria, Iguanidae). Behaviour 57:227–240.

JENSSEN, T. A., AND L. ROTHBLUM. 1977. Display repertoire analysis of *Anolis townsendi* (Sauria, Iguanidae) from Cocos Island. Copeia 1977:103–109.

RAND, A. S. 1967. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. Proc. U. S. Nat. Mus. 122:1–79.

ROTHBLUM, L., AND T. A. JENSSEN. 1978. Display repertoire analysis of *Sceloporus undulatus hyacinthinus* (Sauria, Iguanidae) from southwestern Virginia. Anim. Behav. 26:130–137.

RUBY, D. E. 1977. The function of shudder displays in the lizard, *Sceloporus jarrovi*. Copeia 1977:110–114.

RUIBAL, R. 1967. Evolution and behavior in West Indian anoles. Pp. 116–140 *in* Milstead, W. W. (Ed.), Lizard Ecology: A Symposium. Univ. Missouri Press, Columbia.

SIEGEL, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill Book Co., New York.

STAMPS, J. A., AND G. W. BARLOW. 1973. Variation and stereotypy in the displays of *Anolis aeneus* (Sauria, Iguanidae). Behaviour 47:67–94.

WILSON, E. O. 1975. Sociobiology the New Synthesis. Belknap Press, Cambridge, MA.

Accepted: 28 April 1978

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

Herpetologica, 35(1), 1979, 30–37

FOOD-INITIATED BEHAVIOR OF THE AFRICAN CLAWED FROG (*XENOPUS LAEVIS*): EFFECT OF POPULATION DENSITY[1]

PATRICIA G. FRYE AND VERNON L. AVILA[2]

ABSTRACT: A qualitative and quantitative study was made of food-initiated behavior of the African clawed frog, *Xenopus laevis*. Population densities of 1, 2, 4, and 6 individuals per 38-l aquarium were used. Thirteen selected behavioral components were identified and described. Sequential transitions of these specific behavioral components indicate that an ordered sequence exists for all population densities observed. It was found that (1) both sexes aggregate, (2) food does not elicit stimulation among individuals in groups to the extent that activity increases, and (3) the behavioral patterns of this species are not significantly altered in frequency or sequence by increasing population densities.

Key words: Anura; Behavior; Feeding

INTRASPECIFIC behavioral interactions among feeding animals have been described in leopard frogs (*Rana pipiens*) (Boice and Witter, 1969) and bullfrogs (*Rana catesbeiana*) (Van Bergeigk, 1967). These studies suggest that introducing food into a group of frogs elicits a hierarchical type of behavior (i.e., one individual locates food, then a second individual becomes

[1] This paper is part of a thesis submitted in partial fulfillment of requirements for the M.S. Degree in Biology at San Diego State University.

[2] Please send reprint requests to Vernon L. Avila.