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A description and analysis of male-male interaction behavior in the lizard, Anolis lividus

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A DESCRIPTION AND ANALYSIS OF MALE-MALE INTERACTION

BEHAVIOR IN THE LIZARD, *Anolis lividus*

A Thesis

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Master of Arts

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by

Philip H. Stevenson

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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MASTER OF ARTS

Philip H. Stevenson

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Approved, August 1982

Garnett R. Brooks, Jr.

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Norman J. Fashing

Norman J. Fashing

Stewart A. Ware

Stewart A. Ware

DEDICATION

To Mom and Dad,

who made it possible.

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ABSTRACT

The male interaction behavior of <u>Anolis lividus</u>, endemic to Montsserrat, B.W.I., was described. Laboratory film studies were undertaken which allowed for a quantitative analysis of two display types, type A display and type B display.

Five interaction behaviors were identified; type A display, type B display, dewlapping, sway behavior, and jaw-fencing. A generalized sequence of behavior during an interaction of increasing intensity is: type A display, then type B display, then sway behavior, then jaw-fencing. Dewlapping occurred under highly variable circumstances and is, additionally, a modifier of type B displays. Type A and type B displays are head-bobbing displays. Type A display is the signature display and is stereotyped for movement. Type B displays consist of a sequence of similar head bobs, variable in number.

Sway behavior was a unique display type for three reasons, (1.) it involved horizontally oriented motion, (2.) lizards oriented parallel to each other in mirror image fashion, (3.) lizards would perform this display simultaneously.

The <u>bimaculatus</u> series of <u>Anolis</u> represents a "natural laboratory" for the study of behavior and <u>A. lividus</u> is the first member of this series, which contains <u>23</u> species, to have its social behavior examined.

INTERACTION BEHAVIOR OF MALE *Anolis lividus*

INTRODUCTION

Recently, there has been a great interest in the biology of iguanid lizards, particularly the genus *Anolis*. The genus *Anolis* is important because its distribution represents a "natural laboratory" in many respects,especially in the Caribbean basin. *Anolis* has been divided by Etheridge (1960) into alpha and beta sections; alpha anoles are South American in origin and beta anoles are Central American in origin. Alpha anoles colonized the Caribbean islands from two areas, the southern Lesser Antilles and the central Greater Antilles; beta anoles colonized from the western Greater Antilles (Williams, 1972). The distribution of *Anolis* represents a natural laboratory because of the occurrence of endemic species on many islands and the variable number of species occurring on a given island. Since endemic anoles occur in combinations ranging from more than twenty to one per island, the influence of congeners on their evolution can be tested (Williams, 1969, 1972). The phenomenon of ecological release may also be examined in cases of "solitary" species, a species occurring in the absence of congeners (Williams, 1969). Additional reasons for the interest in Anolis are its ecological diversity, number of species (over 200), conspicuous behavior, diurnal habits, and ease of maintenance in the laboratory. For numerous examples of studies concerned with the biology of this genus see Jenssen (1977a).

Anoles, like other iguanids, use head-bobbing as a means of social interaction. Carpenter and Grubitz (1961) developed the term display-action-pattern, DAP, to describe the pattern of head amplitude change through time which a displaying lizard exhibits, and used graphs of the DAP as a physical representation of the DAP. Jenssen (1977b) determined that DAP's of different species of Anolis have very different levels of stereotypy. Some species having very low stereotypy and others have very highly stereotyped displays. Two other characteristics of DAP's are the degree of complexity (the number and arrangement of motions in a DAP), and the size of the display repertoire (the number of different DAP's a species performs) (Jenssen, 1977b).

This study describes and analyzes these three DAP characteristics as they relate to the behavior of Anolis lividus during male-male interactions. The performance of behavior is considered to be in the challenge context as described by Carpenter (1962). This implies that the displaying animal is interacting with another conspecific under

TABLE 1
bimaculatus SERIES OF Anolis AND ITS
TAXONOMIC BREAKDOWN

TAXA	SPECIES	RANGE
stratulus subseries		
evermani species group		
	evermani	Puerto Rico
stratulus species group		
stratulus subgroup		
	stratulus	Puerto Rico
distichus subgroup		
distichus superspecies		
	distichus	Bahamas
	dominicensis	Hispaniola
brevirostris superspecies		
	brevirostris	Hispaniola
	caudalis	Gonave, Hispaniola
	altavelensis	Alto Velo
	Species A	Hispaniola
bimaculatus subseries		
acutus species group		
	acutus	St. Croix
bimaculatus species group		
bimaculatus subgroup		
	gingivinus	Anguilla Bank
	sabanus	Saba
bimaculatus superspecies		
	bimaculatus	Statia Bank
	leachii	Antigua
marmoratus superspecies		
	nubilis	Redonda
	lividus	Montserrat
	marmoratus	Guadeloupe Bank
	ferreus	Marie Galante
oculatus subgroup		
	oculatus	Dominica
wattsi species group		
wattsi superspecies		
	wattsi	Antigua
	pogus	Anguilla Bank
	forresti	Barbuda
	schwartzi	Statia Bank

TABLE 2
SURVEY OF Anolis FOR WHICH PUBLISHED ACCOUNTS OF MALE INTERACTION BEHAVIOR EXIST

SPECIES	AUTHOR(S)*	TAIL LASHING PRESENT **
aeneus	Gorman, 1968	+
agassizi	Rand et al, 1975	-
allisoni	Ruibal, 1967	-
allogus	Ruibal, 1967	+
biscutiger	Echelle et al, 1971	-
bonairensis	Gorman, 1968	-
carolinensis	Greenberg and Noble, 1944	-
carpenteri	Echelle et al, 1971	-
chlorocyanus	Garcea and Gorman, 1968	-
coelestinus	Garcea and Gorman, 1968	-
cristatellus	Ruibal, 1967	-
cupreus	Echelle et al, 1971	-
garmani	Jenssen, 1977b	-
grahami	Jenssen, 1977b	-
gundlachi	Ruibal, 1967	+
homolechis	Ruibal, 1967	+
humilis	Echelle et al, 1971	-
intermedius	Echelle et al, 1971	+
limifrons	Echelle et al, 1971	+
lineatopus	Ruibal, 1967	+
luciae	Gorman, 1968	+
lucius	Ruibal, 1967	-
nebulosus	Jenssen, 1970	-
pentaprion	Echelle et al, 1971	-
porcatus	Ruibal, 1967	-
richardi	Gorman, 1968	+
roquet	Gorman, 1968	+
opalinus	Jenssen, 1979	-
sericeus	Echelle et al, 1971	-
townsendi	Carpenter, 1962	-
trinitatis	Gorman, 1968	+
tropidolepis	Echelle et al, 1971	-
valincienni	Ruibal, 1967	+

* If more than one citation exists for a species priority given to earliest

** +=tail lashing present

-=tail lashing absent

high conflict or motivational situations as opposed to the assertion context, i.e. low conflict or motivational situations. Both laboratory experiments and field observations were performed with the focus of endeavor being the filming of displays for later analysis. My study is mainly based on films of animals in captivity "since the highest quality films ... of displaying lizards are achieved in the laboratory" (Jenssen, 1977b). Supplemetary field study was undertaken "for contextual information and confirmation of the naturalness of behavior" (Greenberg, 1977).

The species used in this study, Anolis lividus Garman, is endemic to the island of Montserrat, West Indies, and is a solitary species. It is a member of the alpha section, and is sexually dimorphic. Adult males are 3.5 times heavier and 1.5 times longer in snout-vent length, than adult females (G. R. Brooks,pers. comm.). Adult females are generally tan with variable dorsal markings such as chevrons or striping. The color of the typical, active, adult male is bright green with a distinctive orange or red eye ring. Males possess a large, bright yellow, expandable dewlap. For a more complete description see Lazell (1972).

Table 1 records the anoles of close taxonomic relationship to A. lividus, the bimaculatus series (Williams, 1976). By comparing this list with the one in Table 2 note that no anoles within the bimaculatus series, a group of 23 species, have been studied for their social display behavior. Table 1 gives a complete breakdown of the _bimaculatus_ series. Also included are the geographic ranges of the members.

Particularly notable is the _marmoratus_ superspecies, of which _A. lividus_ is a member. These four species, presumed to be very closely related, are solitary species. The four species, _A. ferreus_, _A. lividus_, _A. marmoratus_, and _A. nubilis_, occur respectively on Marie Galante, Montserrat, the Guadeloupe Bank, and Redonda. These four insular localities, although situated near each other, differ greatly in their climatic regimes. This is due in part to their size and geologic origin. Guadeloupe, the largest island, possesses a full range of ecological zonation; and, _A. marmoratus_ has diversified into eleven known subspecies. _A. ferreus_, _A. lividus_, _A. nubilus_ occur on much smaller islands and do not possess identifiable subspecies. This creates an interesting situation in which to examine the influence of ecological factors on the evolution of behavioral displays.

All the anoles of the _bimaculatus_ series would be thought to possess behavioral displays more similar to each other than to members of other series. Some members of the _bimaculatus_ series occur on large islands, Puerto Rico and Hispaniola, with large diverse anoline faunas. Other members occur on smaller islands possessing two to three species. Some members, _A. lividus_ among them, occur strictly as solitary species. This situation represents a unique "natural laboratory" in which to study the evolution of social display behavior.

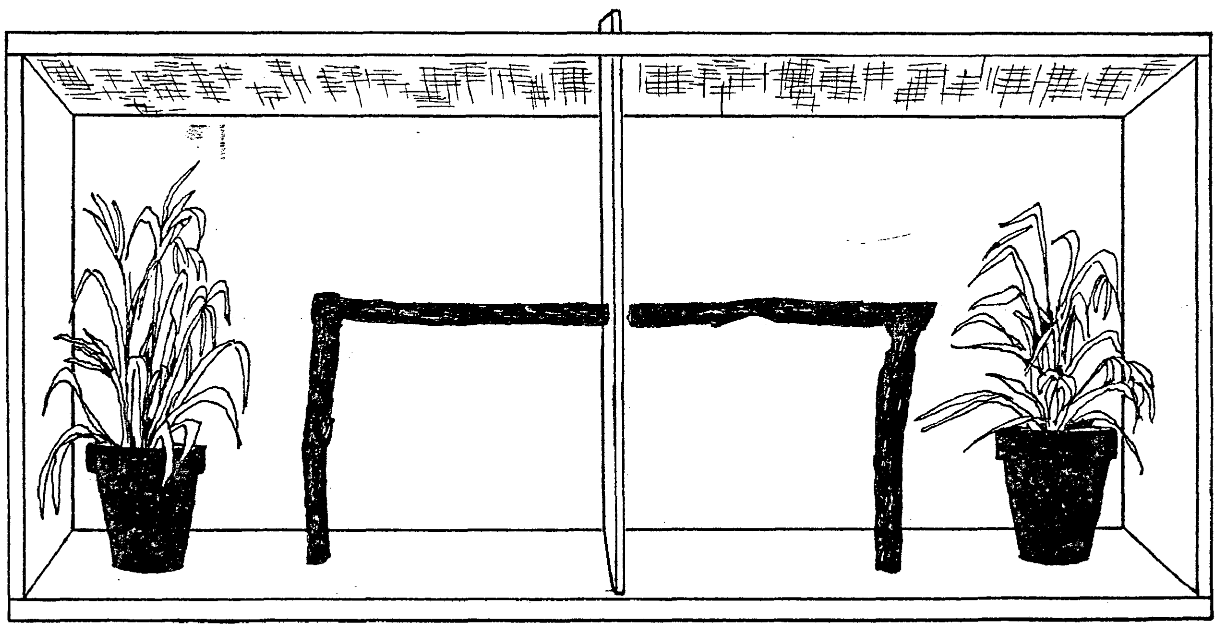
MATERIALS AND METHODS

Information was collected by film studies conducted in the greenhouse of Millington Hall, Williamsburg, Virginia, between October, 1980, and November, 1981 and at the Belham River Golf Course on Montserrat, West Indies, between June 16 and June 24, 1981.

For use in the greenhouse, two cages of plywood measuring 60 cm high by 60 cm wide by 120 cm long were constructed. The front of each cage was a single sheet of plexiglass. The tops of the cages were equipped with two removable screen lids. The interior was painted white for maximum contrast. A removable opaque divider bisected the cage widthwise and protruded above the top of the cage for easy removal when performing trials. The two compartments were each furnished with a green plant and a perch arranged in mirror image fashion (see Figure 1) .

Male lizards were placed one to a compartment and allowed to reside at least six days before a trial was conducted. Trials were conducted by removing the divider and filming the DAP's evoked as the two lizards interacted. A super-8 mm

Figure 1. Diagram of the Experimental Cage



motion picture camera with a zoom lens and a slow motion feature was used. Lizards were initially allowed to interact for 30 minutes before termination of the trial; but this period was later extended to 45 minutes. Filming was done from behind a screen in order to minimize the influence of the camera operator on the lizards' behavior.

When not in the experimental cage, lizards were housed in aquaria provided with plants. The lizards were fed liberally with crickets and watered every 2 to 3 days. Records were kept of lizard snout-vent length (SVL) and weight. All lizards were toe-clipped to ensure individual identification. The fourth toe was not removed from any lizards as it is the largest toe and believed most important in normal climbing abilities. Records were also kept of the housing of lizards. When pairs of lizards were selected for use in trials, one criteria used was the degree of familiarity of lizards. Familiarity was based on the time spent simultaneously in the same housing and the recency of simultaneous housing. Lizard pairs were chosen for least familairity. This was done to ensure maximal interaction of lizards during a trial and to avoid any effects of dominance relationships established during periods of simultaneous housing.

During June, 1981, I traveled to Montserrat to study the lizards under natural conditions. A study site on the grounds of the Belham River Golf Course was located in a triangular area of uncleared vegetation between three fairways. The site offered a variety of vegetation, possessed a moderate population of lizards, and the unique advantage of relative freedom from human interference. A blind was erected on the study site for the purpose of observing and filming lizards without disturbing them. Male lizards were captured, toe-clipped, and color striped for easy identification.

Film analysis was based on the method described by Jenssen (1977c). Head movement was measured using grid units of graph paper onto which film was projected. Graphs were initially constructed using grid units (distance of movement) versus frames of film (time). The camera exposed 18 frames per second; each frame is equal to approximately .056 sec. Frames were kept as the unit of time throughout the analysis because of the heuristic value of this measurement.

Statistics were performed using the IBM 360 Computer and the Prime Computer at the Computer Center of the College of William and Mary; however the Kruskal-Wallis test was performed using a calculator. Sokal and Rohlf (1969) was used as the primary reference text for the selection of statistical analysis; and Rohlf and Sokal (1969) was used as an aid for hand computed statistics. Programming language used was the Statistical Package for the Social Sciences (Nie et al. 1970).

Two readily discernible head-bobbing displays were analyzed. Bob type A consisted of a downward motion followed by a slower upward return motion. An introductory movement was usually present. Bob type A was analyzed by using the duration of the downward motion, measured in frames. Duration of the downward motion was recorded along with the lizard's identification number and the volley in which the display occurred. A volley is defined as a sequence of displays temporally associated and distinctly separate from other such volleys. A Kruskal-Wallis test was performed using lizard as the classification and duration of downward motion as the variable. The raw data is recorded in Appendix I. Correlation analysis was performed to determine any relationship between length of downward motion and chronological order of display within a volley. Descriptive statistics were also produced for length of the downward motion.

The second type of head-bobbing display, type B display, was analyzed differently due to quantitative and qualitative differences in the display. The type B display consisted of a variable number of head bobs, all of similar type. The bobs within a type B display generally required one frame to reach the point of minimum amplitude with the head immediately returning upward. The head would occasionally continue to move after the initial downward motion and following return; but, this is attributed to an elastic rebound effect as the continued motions were of lessening amplitude. The inter-bob pause, henceforth abbreviated IBP, was measured within each display. An IBP is the time interval, measured in frames, between the initial downward motion of a head bob and the initial downward motion of the following bob. Appendix II presents several samples to illustrate this analysis. For all type B displays, the lizard performing the display, the volley in which it occurred, the number of bobs present, the IBP's, the total length of the display, and the intra-volley pause were recorded.The intra-volley pause is the time interval between displays in a given volley. Descriptive statistics of bob number per display, IBP length, and IVP length were produced.

Displays having 3, 4, 5, and 6 bobs were present in large enough numbers to be analyzed in more detail. The analysis will be described in the Results section. All ANOVA were performed on homoscedastic samples unless otherwise specified. All ANOVA performed on heteroscedastic samples were repeated using the Kruskal-Wallis test. Several correlation studies were performed. All correlation studies presented will provide the nonparametric correlation coefficients, Spearman's correlation coefficient and Kendall's correlation coefficient. Pearson's correlation coefficient is not presented as the variables involved did not meet the assumptions for this method.

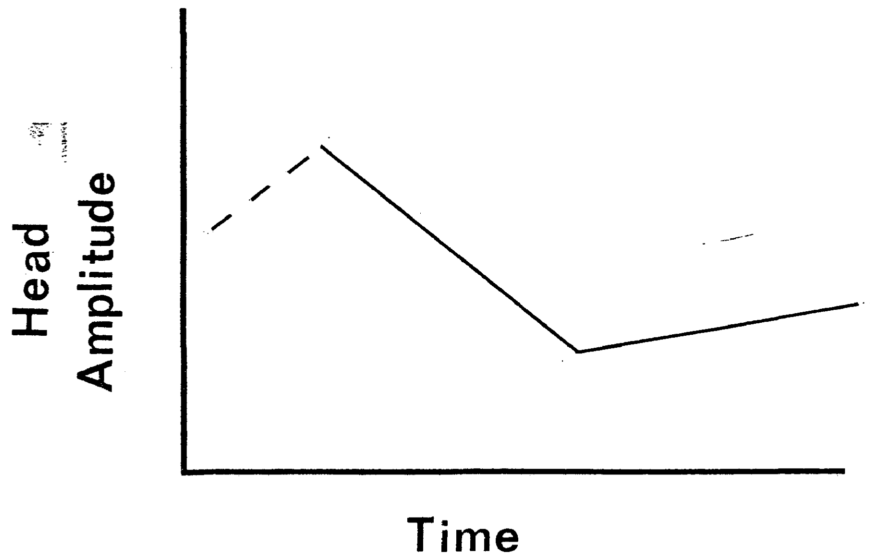
RESULTS

To facilitate understanding of the information provided, this section has been divided into two portions. The first portion, observational notes, will describe all male social interaction behaviors observed and their occurrence during interactions. Also described will be the overall pattern of interaction and the determinaton of dominance during territorial disputes. The second portion, statistical analysis, will present the descriptive statistics and analyses performed on the data collected via film studies for the type A and type B displays.

I. OBSERVATIONAL NOTES

The type A display was found to exhibit a very similar pattern among all lizards in which it was filmed; observations of this display also did not reveal any inconsistencies. Figure 2 shows a generalized type A display. The vertical axis is relative head position and the horizontal axis is time. No units are specified. There is an upward introductory movement which was present in 49 of 53 filmed type A displays. This is

Figure 2. DAP Graph of the Type A (Signature) Display


Head Amplitude
Time

the dotted portion of the curve. The next movement, a downward motion, was of variable length. The return motion upward was slower than the downward motion and of variable length. This motion did not always cease when the head was at the same level as when motion started. Frequently, the return upward was quite abbreviated.

The type A display is observed under more variable circumstances than the type B display. During lab trials, this display was usually performed first when the lizards were at a maximal distance from each other and was not performed when the interaction between males became more intense. The display has been observed in the wild and in the laboratory when the displaying male was not in the presence of other males; then it is occurring in the assertion context (Carpenter, 1962). The type A display appears to be what is known as the signature bob (Stamps and Barlow, 1973). Jenssen (1977b) defines signature display for anoles possessing more than one display pattern as that display which occurs in a context in which there is little or no social interaction. The signature display appears to be stereotyped for movement, but not necessarily for length of the movements with regard to time.

The type B display is a series of similar bobs, variable in number, given during higher intensity situations than type A display. The type B display is typically observed when a male lizard is approaching another male and the interaction has intensified. This display was not observed in the assertion context as was the signature display; however it was observed in nature during courtship, a context other than inter-male aggression. It is very interesting that this display would occur during both aggressive interactions and courtship.

There is one aspect of anoline display behavior not previously discussed, and that is modifiers. A display modifier is a posture or body movement not always present with a display (Jenssen, 1977a). Modifiers may be dynamic (additional movement), or static (postural changes). Many modifiers have been observed in anoles. Anolis lividus does not exhibit many of the modifiers observed in other anoles. This species will raise the nuchal crest along the dorsal side of the neck, engorge the area beneath the jaw and swell its body, but does not protrude its tongue or gape explicitly.

During inter-male interactions, typically the crest is raised and the throat gorged. Both signature display and type B displays would possess these postural changes; but only for the signature display would they constitute modifiers as this display occurs outside of the aggressive context when these modifiers are not present.

Dynamic modifiers are the variable movements associated with display types. Type B display exhibits some variability in the intensity of performance. The head bobs typically involve motion of the neck and limited motion of the forelegs;

however, vigorous bobbing may involve greater movement of the forelegs and even involve some limited motion of the hindlegs. Conversely, only the neck may be involved in the head bobbing of the type B display.

The signature bob was observed to possess a variable introductory movement which was present in the majority of signature displays. Signature bobs also exhibited some variation of the intensity of movement involved. The upward movement following the downward movement was quite variable in the extent to which the head would be raised. Another modifier observed with the signature display was a shuffling walk during the performance of the downward motion of the display. This walk modifier was only observed during signature displays performed in the challenge context, and it was not typically present. The walk would start in conjunction with the downward motion and cease when the lizard's head had reached the point of minimum elevation; however, the display appeared to be essentially unaltered.

One particular form of dynamic modifier must be considered seperately as it also represents a discrete display type- this is dewlapping. Dewlapping involves the extensiion of the typically brightly colored throat fan and its subsequent withdrawal. Dewlapping is a highly prominent feature of anoline behavior. The potential signal value of dewlapping is readily understood; however, this behavior is ubiquitous with regard to context. It may appear as a discrete display type or as a display modifier. Dewlapping occurs in both assertion and challenge contexts and may be elicited by many different stimuli, e.g., other lizards, feeding, or approach of observer.

Dewlapping occurs frequently during inter-male interactions, with some important limitations. Dewlapping may occur prior to or following a signature display but never during a signature display. Dewlapping was observed to occur before, during and after a type B display, with no obligate relationship apparent. Dewlapping typically involves the pulsing of the dewlap at a fairly rapid rate (about once a second or less); however, there was observed a display type in which the dewlap was held extended.

Sway behavior was a form of display unique to A. lividus. It was not observed frequently enough for statistical analysis but a descriptive account of the behavior will be undertaken. Sway behavior was observed during intensely aggressive interactions. Males approach each other during aggresive interactions through a series of movements and pauses. When males came in to close proximity to one another, sway behavior would sometimes occur. Males were generally separated by approximately 0.2 m. No exact measurements were taken; this distance is estimated from a review of film in which sway behavior was recorded. Sway behavior was not observed in all intense interactions.

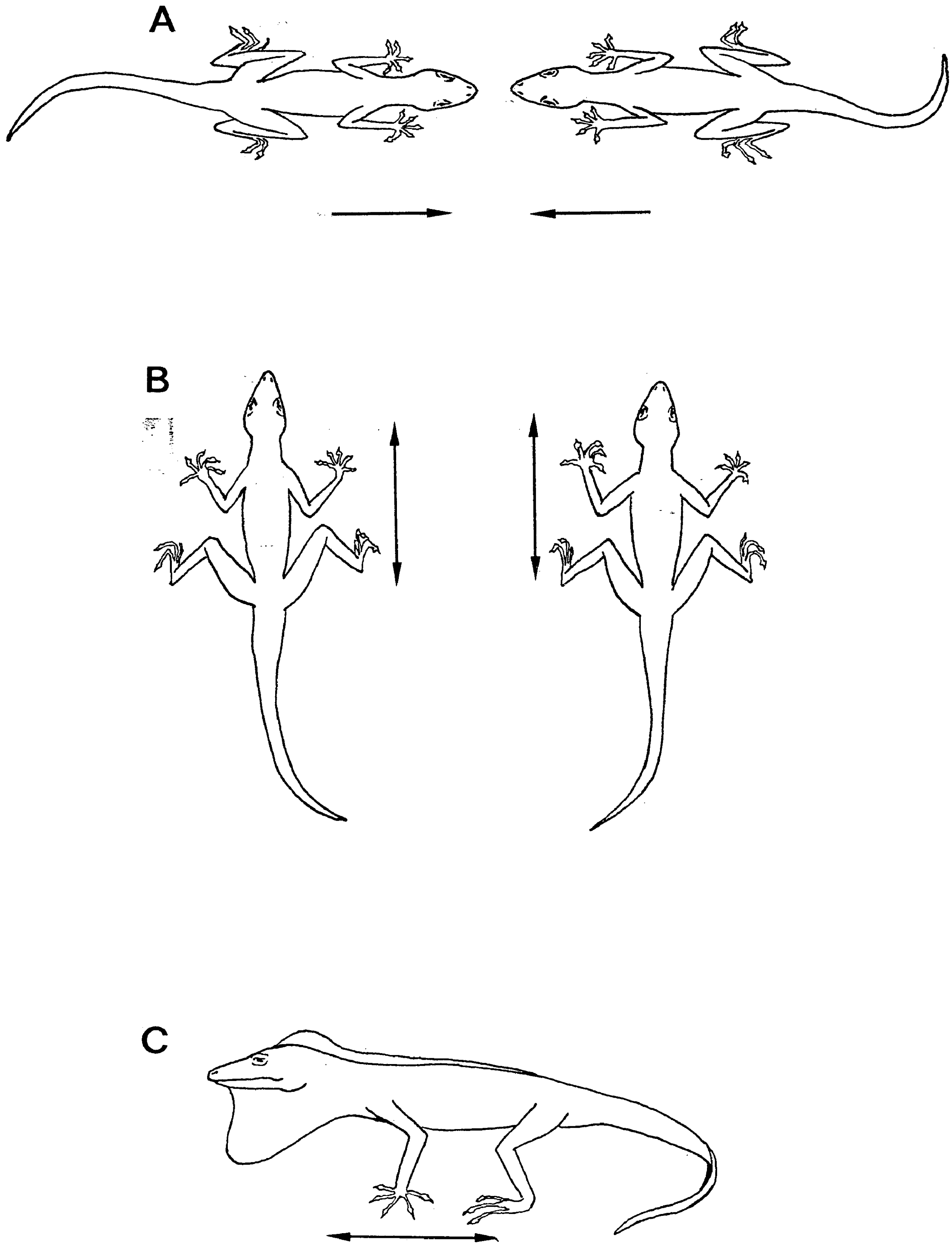
ORIENTATION AND MOTION DURING SWAY

Figure 3a. Lizards in Approach Orientation

Figure 3b. Lizards During Sway Display

Figure 3c. Profile of Lizard During Sway Behavior

(Arrows indicate direction of motion.)


A
B
C

Sway behavior starts with the displaying male turning and orienting at a right angle to the direction of approach (Figure 3a and 3b). The dewlap is extended and held extended while the lizard begins to rock backward and forward (Figure 3c). Jenssen (1977a) discusses evolutionary reasoning for social displays to be oriented along the vertical axis. Sway behavior, involving motion along the horizontal axis, is highly unusual. Of the 33 anole species whose behavior have been studied to some extent (listed in Table 2), only _A. nebulosus_ is reported to have a display with horizontally oriented motion (Jenssen, 1970). Only one other lizard, _Phenacosaurus richteri_, is reported to have a rocking motion dispay (Kastle, 1965).

Another interesting aspect of sway behavior is that if one male begins a sway dispay the male with which it is interacting will almost simultaneously begin a sway display. Furthermore, when two males are performing sway behavior they are oriented parallel to each other in mirror image fashion. Carpenter (1967) describes displaying iguanid lizards as performing challenge displays oriented head to tail. The Jamaican anole, _A. opalinus_, has been reported to have an orientation similar to the one described for _A. lividus_ (Jenssen, 1979). At the cessation of sway behavior, a type B display is frequently performed.

One additional behavior occurring during male interactions remains to be described, and that is jaw-fencing. Two interacting males interlock their jaws and then move forward and backward while interlocked. This is the highest intensity of male interaction. The interacting lizards will have approached each other very closely. Usually one male will lunge and gape at the other; the other male will interlock his jaws with those of his opponent. The head of each lizard is rotated approximately forty five degrees. Of 9 bouts of jaw-fencing filmed, it was noticed that 7 times the males rotated their heads to the right. It would be interesting to obtain more extensive information on the right-left orientation of the head during jaw-fencing to see if there is a preference.

Males appear to exert a great deal of force to attempt to dislodge their opponent during jaw-fencing. Each male will have its throat gorged and nuchal crest raised. The body appears swollen and is pressed against the substrate, apparently for maximal purchase to the perch. Dewlapping never occurs during jaw-fencing.

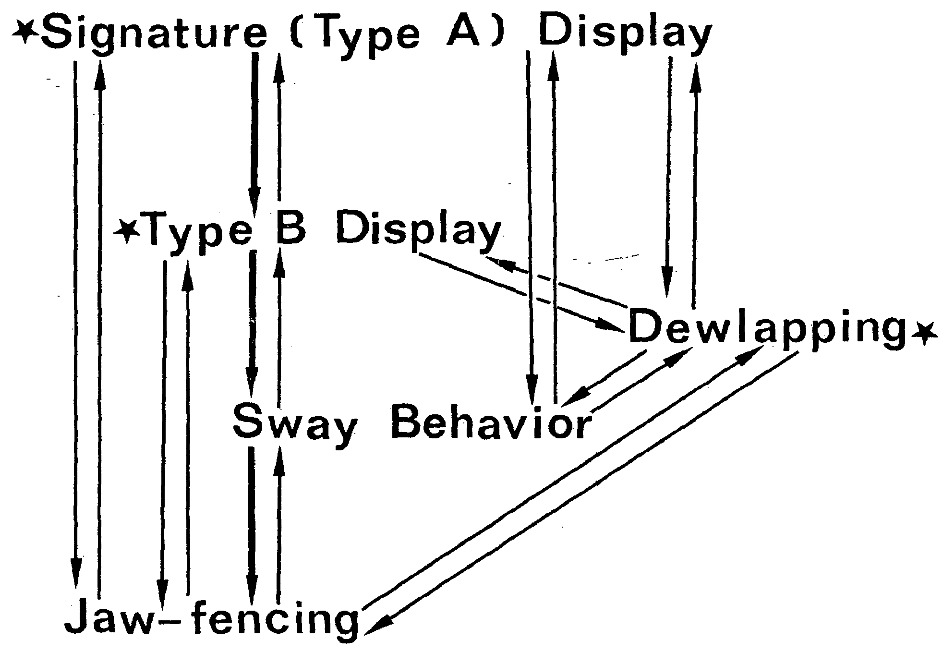
During jaw-fencing there may be periods of quiescence. During periods of quiescence, the lizards may remain interlocked or may withdraw from the grip. If males remain interlocked there may be a noticable relaxation of their grip. Type B dislays may be performed during periods of quiescence, without dewlapping.

One form of behavior that has been reported for other anoles is absent in _A. lividus_; that is tail lashing (Echelle et al. 1971; Gorman, 1968; Ruibal, 1967). I observed no behavior in _A. lividus_ which would constitute tail lashing. Table 2 indicates the species for which tail lashing has been reported.

Now that all male interaction behaviors have been mentioned, a generalized sequence of male interaction behavior can be developed. Figure 4 is a representation of the sequences of behavior. Arrows point to behaviors which may possibly occur after the behavior where the arrow originates. The star next to dewlapping, signature display, and type B display, indicates that these displays are possible first displays during the initiation of an interaction. The heavy arrows indicate the generalized sequence of behaviors from least intense to most.

After removal of the divider during a laboratory trial, the first reaction of a male upon seeing the other male is to raise the nuchal crest and gorge the throat. Both of these postural changes do not obligately occur together. The first behavioral display is usually dewlapping or signature display. As the lizards begin to approach each other, displays continue to be given. There seemed to be a tendency that once a male began performing the type B display it would cease to perform the signature display. If one male is performing type B display this does not necessarily mean that the other male will

Figure 4. Representation of Behavioral Sequence During Male Interactions



*Signature (Type A) Display
*Type B Display
Dewlapping*
Sway Behavior
Jaw-fencing

not continue to perform the signature display if it is doing so. Generally, as the interaction intensifies, both males will be performing the type B display. This was observed both in the lab and in the field.

If males continue to approach one another, sway behavior may occur. Sway behavior is typically followed by a type B display while still in the sway orientation. Dewlapping may also occur after sway behavior. The signature display was not observed after sway behavior in an interaction which was still intensifying. When one male returns to the approach orientation the other male does also.

Jaw fencing will now occur. If the two lizards are at close proximity when performing sway behavior, they may engage in jaw-fencing immediately after sway behavior. Jaw fencing usually results in one male becoming dominant. Jaw fencing was not observed by the author in the field but has been reported to occur (Brooks, pers. com.). If jaw-fencing was interrupted before dominance was established, e.g., one lizard falling off the perch, lizards would continue to display at each other. Type B display, dewlapping, sway behavior, and an eventual resumption of jaw-fencing may occur.

The determination of dominance may occur at any time during an interaction. In fact, one male may not challenge the other male from the start. An interaction may procede for several minutes then cease when one males yields to the other before actually engaging in jaw-fencing. The subordinate male will typically avoid the dominant male. Newly subordinate males do not typically exhibit a raised crest and gorged throat. Occasionally, a subordinate will perform a few displays after dominance has been determined. Subordinate males will frequently change color to a drab brown.

II. STATISTICAL ANALYSIS

SIGNATURE DISPLAY (TYPE A)

The signature display is composed of primarily a single feature, the downward motion. This feature of the signature display is the most consistent aspect of the display. The introductory motion, variable in presence, did not exhibit any noteworthy variation in length. The return motion upward was quite variable in length and height at which it ceased. This portion of the signature display was considered to be derivative from the downward motion and merely a repositioning of the head in preparation for future behavior. Consequently, descriptive statistics were not produced for the upward movement as insufficient information with regard to following behavior was available. Another reason of equal importance is that, due to the variability of the upward motion, there exists a great deal of ambiguity as to which upward motions constitute part of the display and which do not.

Figure 5. Bar Diagram of Length of the Downward Motion for the Signature Display

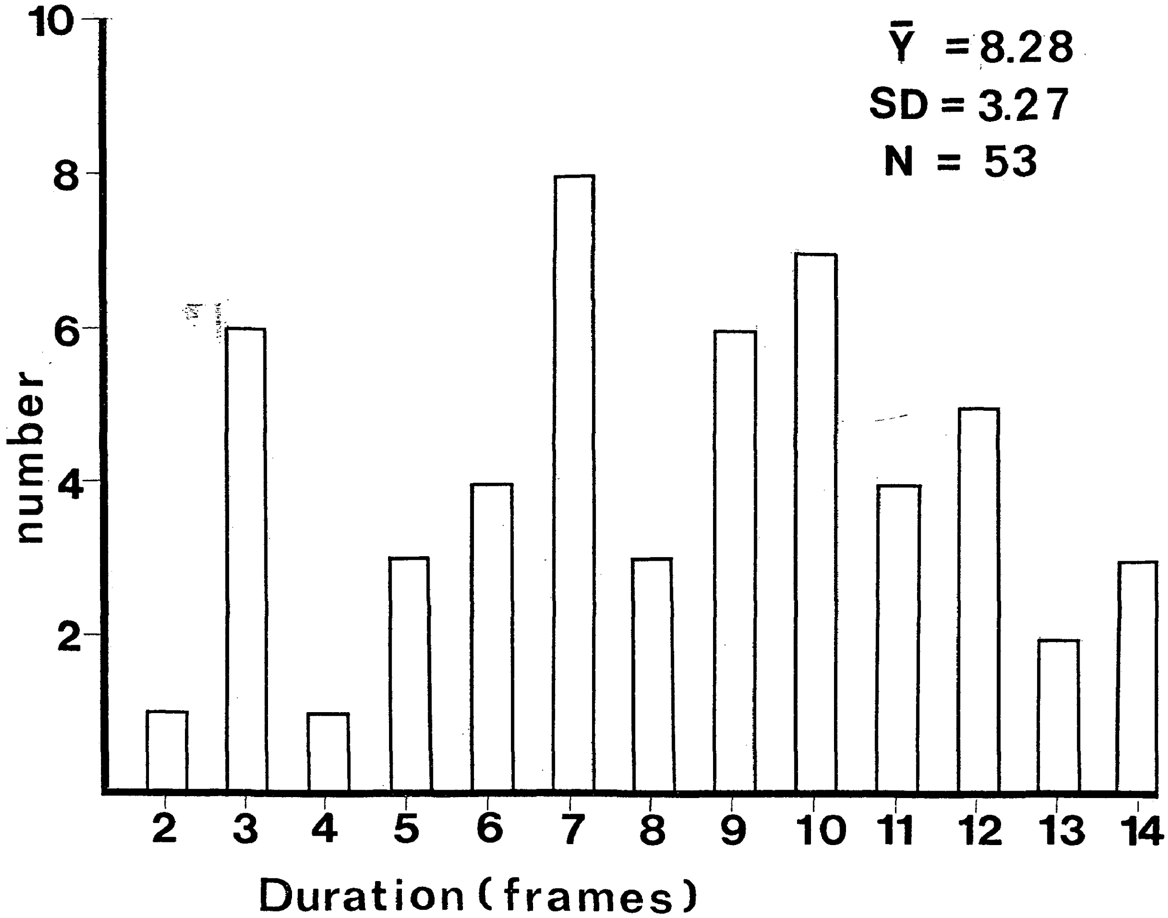

$\bar{Y}$ = 8.28
SD = 3.27
N = 53
10
8
6
4
2
number
2
3
4
5
6
7
8
9
10
11
12
13
14
Duration (frames)

Figure 5 is a bar diagram of the number of signature displays in which the downward motion is of a given length. As stated previously, all measurements of time are in frames (1 sec.= 18 frames). The mean length of the downward motion was 8.28 frames and the standard deviation was 3.27 frames.

A Kruskal-Wallis test was used to compare the length of downward motion between different lizards. An ANOVA was not used as the assumption of homoscedasticity was not met. The result of the Kruskal-Wallis test was that the individual lizards' signature displays possessed significantly different lengths of the downward motion ($p < 0.005$). This could allow for individual recognition via the length of the downward motion.

It was noticed that the length of the downward motion seemed to increase during a given volley. The results of a correlation study indicated that there is a significant relationship between position of display within a volley and the length of the downward motion. Both Kendall's and Spearman's correlation coefficients were computed. Kendall's correlation coefficient is 0.2539, and Spearman's correlation coefficient is 0.3390. Both coefficients were highly significant ($p < 0.01$).

TYPE B DISPLAY

Figure 6 is a bar diagram of the number of bobs per

Figure 6. Bar Diagram of the Bobs per Display for the Type B Display

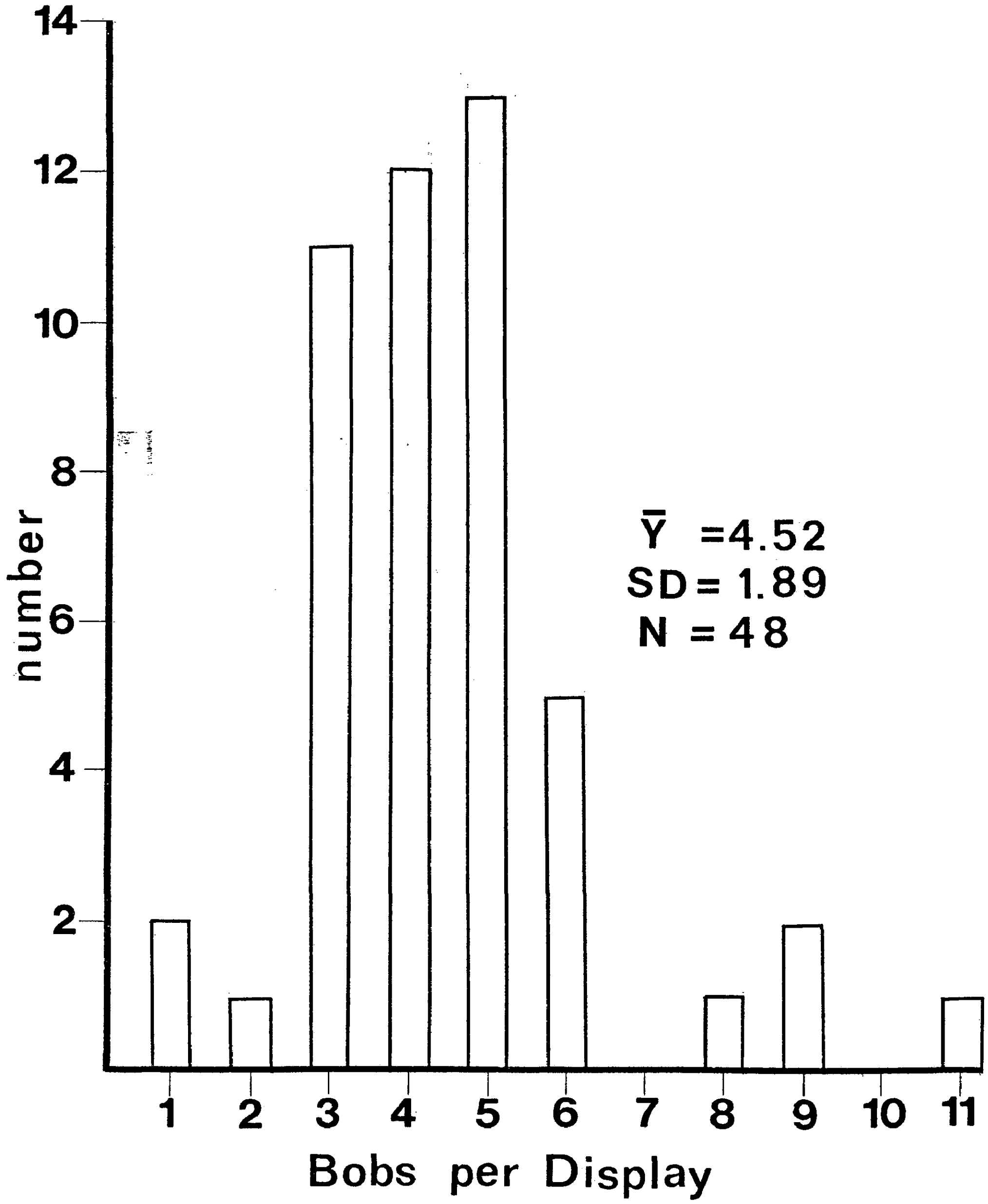
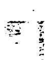
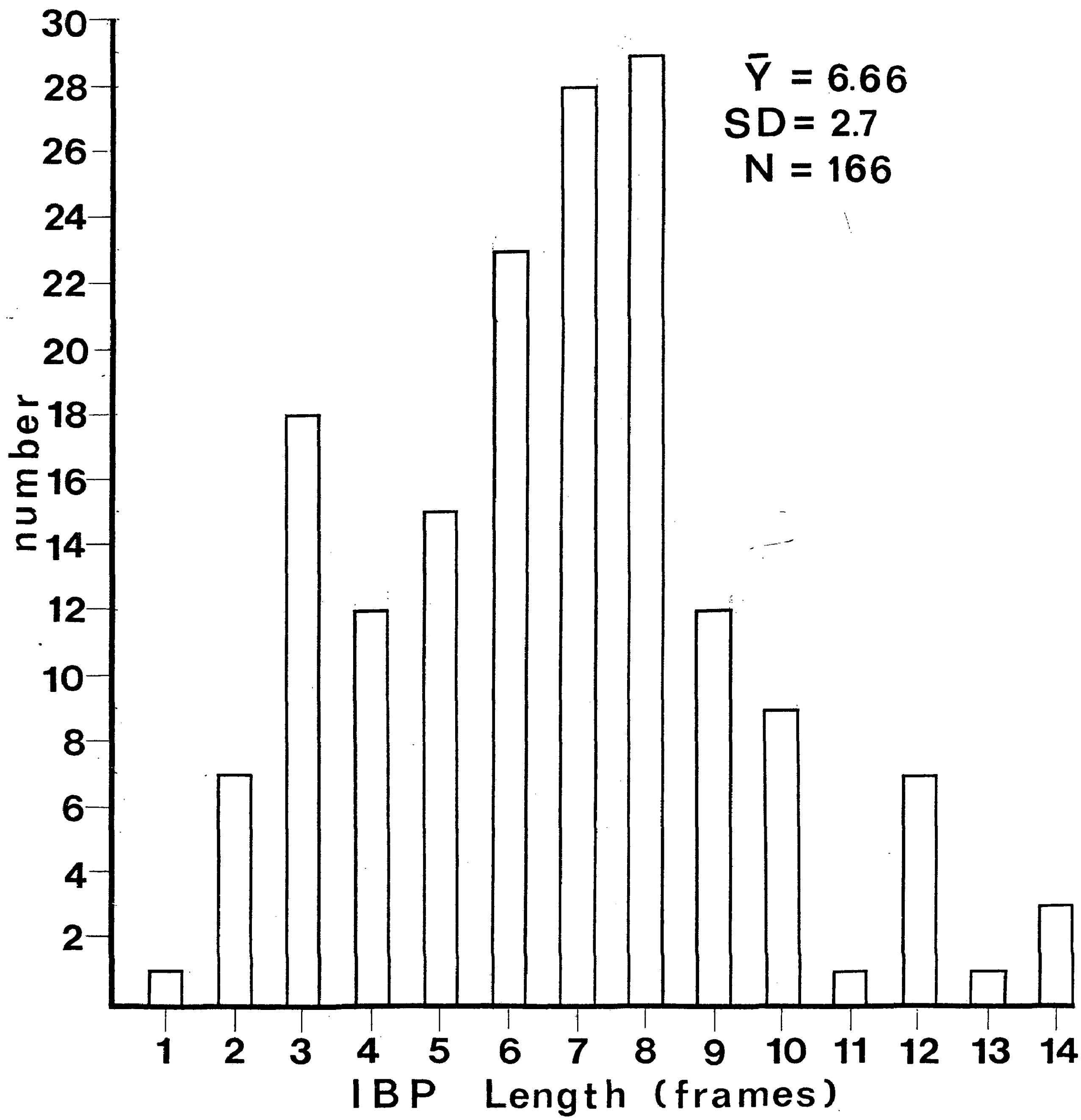

14
12
10
8
6
4
2
number
Ȳ =4.52
SD= 1.89
N = 48
1
2
3
4
5
6
7
8
9
10
11
Bobs per Display

Figure 7. Bar Diagram of the Inter-Bob Pause



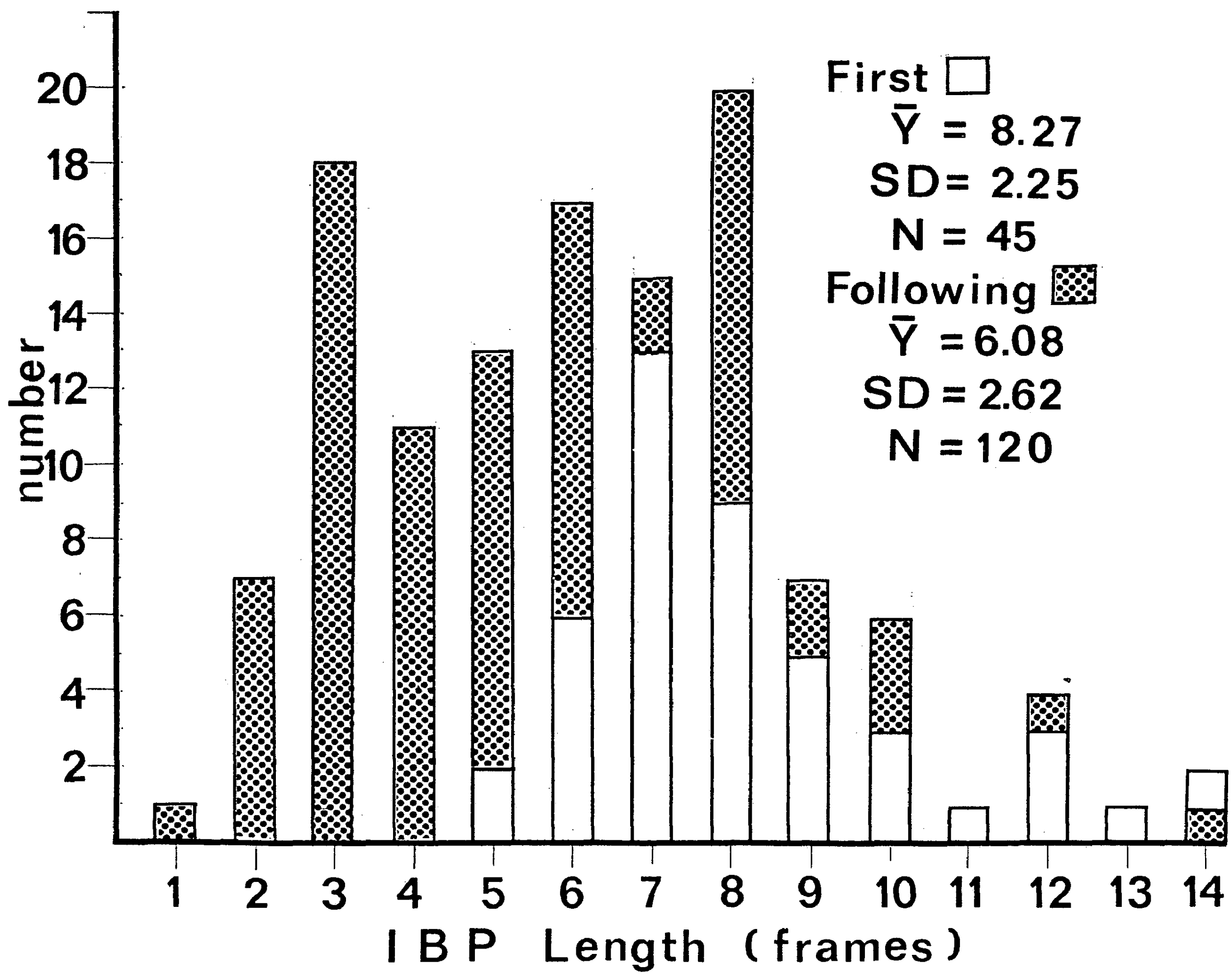

Ȳ = 6.66
SD= 2.7
N = 166
number
IBP Length (frames)

display. The vertical axis is the number of displays and the horizontal axis is the number of bobs per display. The mean number of bobs per display is 4.52 and the standard deviation is 1.89. The total number of displays is 46.

The inter-bob pause data is displayed in Figure 7. The length of the inter-bob pauses is the horizontal axis and the number of IBP's of given length is the vertical axis in this bar diagram. The mean IBP length is 6.7 frames and the standard deviation is 2.7 frames. It was learned during analysis that the minimum IVP, intra-volley pause, and the maximum IBP were very close in length. This introduces some ambiguity as to what constitutes the division between displays. Displays had been subjectively determined during normal speed projection of the films. Since there was a discrete gap between the sample of IBP's and the lowest IVP, this gap was tested comparing the lowest IVP to the sample of IBP's. The sample of IBP's is normally distributed and a t-test was used. The lowest IVP was found to significantly differ from the sample of IBP's ($p < 0.01$).

The first series of analyses concerned the differences in IBP lengths within the sample. It was initially observed that the first pause seemed to be longer than the following IBP's. A oneway ANOVA was run in which the first IBP of all displays possessing greater than one IBP were pooled and compared to the pooled sample of all nonfirst IBP's for all displays possessing

Figure 8. Bar Diagram of First IBP and Following IBP


First
$\bar{Y}$ = 8.27
SD= 2.25
N = 45
Following
$\bar{Y}$ = 6.08
SD = 2.62
N = 120
number
2
4
6
8
10
12
14
16
18
20
1
2
3
4
5
6
7
8
9
10
11
12
13
14
I B P Length (frames)

greater than one IBP. Figure 8 represents the two samples in the form of a bar diagram. The means are highly significantly different ($p < 0.001$).

With this difference so distinct, a search was begun for other relationships between IBP length and position within the display. It was initially decided to disregard all other displays except those containing 2, 3, 4, and 5 IBP's, i.e., displays possessing 3, 4, 5, and 6 bobs. Referring to Figure 6, it will be observed that the chosen displays represent the bulk of the sample and that the number of displays for the specified classes may be large enough to perform meaningful analyses.

The data for the specified displays appears in Table 3. The descriptive statistics for the IBP's by position and display classification are given. Display classification is based on the number of IBP's per display; and the number of displays of a given class is recorded next to the display class. For each chronological position in a given display class, the mean IBP and the standard deviation are given. A dash indicates that there were no IBP's present at that position, e.g., displays containing 4 IBP's do not have any IBP's in the fifth position. Note the general tendency for IBP length to decrease during a display. Table 4 shows the pooled data for the 2, 3, 4, 5 IBP displays. For each position the number of IBP's occurring at that position, the mean of the

TABLE 3
POSITIONAL IBP DATA BY DISPLAY CLASS
(2, 3, 4, and 5 IBP displays)

N	DISPLAY CLASS	FIRST $\bar{Y}$	FIRST SD	SECOND $\bar{Y}$	SECOND SD	THIRD $\bar{Y}$	THIRD SD	FOURTH $\bar{Y}$	FOURTH SD	FIFTH $\bar{Y}$	FIFTH SD
11	2 IBP	8.45	2.25	5.82	3.74	-	-	-	-	-	-
12	3 IBP	8.08	2.39	7.08	1.24	4.33	2.19	-	-	-	-
13	4 IBP	8.15	1.77	7.15	1.77	5.69	1.80	4.15	2.58	-	-
5	5 IBP	7.00	0.71	7.40	2.79	6.60	2.30	6.20	1.79	5.00	1.87

TABLE 4

IBP's FOR 2, 3, 4, AND 5 IBP DISPLAYS POOLED BY POSITION

IBP POSITION	N	$\overline{Y}$	SD
FIRST	41	8.07	2.00
SECOND	41	6.80	2.45
THIRD	30	5.30	2.15
FOURTH	18	4.72	2.52
FIFTH	5	5.00	1.87

TABLE 5
RESULTS OF ONEWAY ANOVA COMPARING POSITIONAL IBP
(for 2, 3, 4 and 5 IBP displays and pooled sample)

SAMPLE	F-RATIO	PROBABILITY	DF BETWEEN	DF WITHIN
POOLED	10.713	0.0001	4	130
2 IBP	4.016	0.0588	1	20
3 IBP	11.270	0.0002	2	33
4 IBP	9.808	0.0001	3	48
5 IBP	1.044	0.4093	4	20

IBP's in the given position, and the standard deviation are recorded.

Utilizing this data, oneway ANOVA were performed for each display class and the pooled sample. The classification within each ANOVA was position. Table 5 displays the results. For each sample, the information used, the calculated F-ratio, and the probability are recorded. Only two of the ANOVAs did not yield significant results, the ANOVA for 2 IBP displays and the ANOVA for 5 IBP displays. However, the ANOVA for 2 IBP displays is very close to significance. The 5 IBP display ANOVA's probability is large; but, the small sample size hinders the analysis here.

Tests for the presence of significant subsets were run simultaneously with the ANOVAs. For the 2 and 5 IBP displays, there were no significant subsets as the ANOVAs did not indicate heterogeneity of means. The significant subsets are displayed in Table 6. The subsets are indicated by the position of the IBP written as numbers on the same line. The pooled sample indicates that the first IBP is significantly different than the other IBP's reiterating what occurred in the initial ANOVA. The other two subsets are difficult to interpret. For the 3 and 4 IBP displays it is notable that the first IBP's are not significantly different than the second IBP's.

The trend which is most interesting as illustrated by the

TABLE 6

SIGNIFICANT SUBSETS FOR EACH ANOVA IN TABLE 5

SAMPLES:	POOLED	2 IBP	3 IBP	4 IBP	5 IBP
	1	NONE	1,2	1,2	NONE
	2,3,4		3	2,3	
	2,3,5			3,4	

TABLE 7

RESULTS OF ANOVA's COMPARING POSITIONAL IBP ACROSSS DISPLAY CLASS
(for 2, 3, 4, and 5 IBP displays)

POSITIONAL IBP	F-RATIO	PROBABILITY	DF BETWEEN	DF WITHIN
FIRST	0.599	0.6198	3	37
SECOND	*	approx. 0.5	-	-
THIRD	2.597	0.0930	2	27
FOURTH	2.615	0.1254	1	16

* heteroscedastic, Kruskal-Wallis test used.
Adjusted H = 2.242 compared to chi-square with 3 df.

significant subsets of the 3 and 4 IBP displays is the ordering of the subsets chronologically. Only adjacent IBP's are similar. From the raw data presented in Table 3, this is not surprising.

Oneway ANOVA were also performed comparing given positional IBP's between display types, e.g., ANOVA comparing the first IBP's of the four display classes. The results are displayed in Table 7. No significant differences were found. The samples of second IBP's was not homoscedastic; therefore, a Kruskal-Wallis test was used to compare the samples of second IBP's. The result was not significant.

To further examine the relationship between position and IBP length, an ANOVA comparing three samples was run. The samples were taken from displays containing 3, 4, 5 IBP's. The samples were first IBP's, last IBP's, and intervening IBP's which will be referred to as middle IBP's. The 2 IBP displays were not initially used as they possess no IBP's in the middle position but were included in a separate ANOVA later. The result of the oneway ANOVA comparing first, middle, and last IBP's was highly significant ($p < 0.001$) indicating that the three samples are not homogeneous. A similar ANOVA was performed with a slightly larger sample composed of all displays containing three or more IBP's from which to draw the three classes. The result of this ANOVA was also highly significant ($p < 0.001$) indicating heterogeneity of subsets.

TABLE 8

RESULTS OF ONEWAY ANOVA's COMPARING FIRST, MIDDLE, AND LAST IBP
(subset means provided)

DISPLAY IBP's DRAWN FROM	F-RATIO	PROBABILTY	SUBSET MEANS FIRST	MIDDLE	LAST
3,4,5 IBP	24.455	0.0001	7.93	6.62	4.37
2,3,4,5 IBP	*	0.01	8.07	6.62	4.75
>2 IBP	23.586	0.0001	8.32	6.71	4.58
>=2 IBP	24.039	0.0001	8.36	6.71	4.89

* heteroscedastic, Kruskal-Wallis test performed.

Adjusted H = 41.614 compared to chi-square with 2 df.

Duncan multiple range tests were simultaneously performed with the above ANOVA, and established that the three subsets, first IBP, middle IBP, and last IBP, are each significant subsets. Table 8 records the F-ratio and its significance for both of the above ANOVAs and the individual subsets' mean, standard deviation and number of variates.

Also recorded in Table 8 are the results of two further ANOVA identical to the two described above except that the IBP's from displays containing 2 IBP's were added to the subsets. 2 IBP displays possess IBP's only in the first and last position. The analysis for first, middle, and last IBP in which the data were drawn from the 2, 3, 4, and 5 IBP displays was performed by Kruskal-Wallis tests as the subsets are heteroscedastic. The result was that the subsets are significantly different ($p < 0.01$). The other analysis was performed by oneway ANOVA and the subsets were drawn from all displays containing 2 or more IBP's. The result is that the subsets differ significantly ($p < 0.001$). A Duncan's multiple range test was also performed and revealed that the three subsets, first, middle, and last, each represent a significant subset.

Since there appears to be some relationship between IBP length and position within the display, a correlation analysis was performed. Both Kendall's and Spearman's correlation coefficients were computed. The values of Kendall's

TABLE 9
CORRELATION OF IVP AND FOUR VARIABLES
(with descriptive statistics)

VARIABLES	$\overline{Y}$	SD	CORRELATION COEFFICIENTS SPEARMAN'S VALUE	PROBABILITY	KENDALL'S VALUE	PROBABILITY
IVP	33.08	17.06	–	–	–	–
PREVIOUS DISPLAY TOTAL LENGTH*	28.64	16.36	0.013	0.470	0.020	0.435
FOLLOWING DISPLAY TOTAL LENGTH*	23.39	9.15	0.130	0.225	0.087	0.234
PREVIOUS DISPLAY BOB TOTAL	4.61	1.95	-0.104	0.273	-0.070	0.292
FOLLOWING DISPLAY BOB TOTAL	4.00	1.20	-0.045	0.397	-0.028	0.415

* measured in frames.

coefficient and Spearman's coefficient are −0.301 and −0.381 respectively. Both coefficients are highly significant ($p=0.001$).

The next analysis performed involved the intra-volley pause, IVP. The descriptive statistics for IVP are recorded in Table 9. Also recorded in Table 9 are the variables which IVP was correlated with and their descriptive statistics. The IVP was examined for correlation with four variables: the length of the display preceding each pause, the length of the display following each pause, the number of bobs in the display preceding each pause, and the number of bobs in the display following each pause. Both Kendall's and Spearman's correlation coefficients were computed for the relationship between IVP and the four variables. The values for the correlation coefficients and their significance appear next to the four variables in Table 8. As can be seen from the results in Table 9, there are no significant correlations between any of the four variables and IVP. This seems to indicate IVP length is independent of the length and bob number of the displays which bracket the pause. The results of a correlation study of the relationship between IVP and its position in the volley are displayed in Table 10. Both Kendall's and Spearman's correlation coefficients were highly significant ($p = 0.002$) and have values of 0.3721 and 0.4683 respectively.

The last analysis performed was a search for patterns

TABLE 10

RESULTS OF CORRELATION BETWEEN IVP AND ITS POSITION WITHIN A VOLLEY

CORRELATION COEFFICIENT	VALUE	PROBABILITY
SPEARMAN'S	0.468	0.002
KENDALL'S	0.372	0.002

TABLE 11

CORRELATION OF DISPLAYS PER VOLLEY AND THREE VARIABLES

	CORRELATION COEFFICIENTS			
	SPEARMAN'S		KENDALL'S	
VARIABLE	VALUE	PROBABILITY	VALUE	PROBABILITY
MEAN IVP	0.539	0.044	0.473	0.029
MEAN BOBS PER DISPLAY	-0.608	0.018	-0.490	0.019
MEAN DISPLAY TOTAL LENGTH	-0.464	0.064	-0.335	0.76

among the volleys. A correlation study was performed, again using Kendall's and Pearson's correlation coefficients. The number of displays per volley was compared with the mean IVP, the mean number of bobs per display, and the mean total length of displays. Table 11 displays the descriptive statistics for each variable. Also recorded in Table 11 are the two correlation coefficients and their significances. The coefficients are recorded on the same line as the variable which was paired against displays per volley. Both mean IVP and mean bobs per dispaly do have a significant correlation with displays per volley. Mean display length does not possess a significant correlation with displays per volley. Mean IVP is positively correlated with displays per volley and mean bob number per display is negatively correlated with displays per volley.

DISCUSSION

Anolis lividus possesses two head-bobbing patterns of which one is stereotyped for motion and one is not. The signature display was found to be stereotyped for the general sequence of movements performed, but not for the duration of the movements. This appears very similar to what has been observed in Anolis nebulosus. This anole possesses a highly stereotyped signature display which each individual performs with a highly specific, different duration (Jenssen, 1971). Since in A. lividus, there is significant variability between lizards in the duration of their signature displays, individual recognition is possible. The significance of individual recognition is that more "efficient" behavior is possible. In cases in which lizards share an established dominance relationship, individual recognition would allow subordinates to desist from engaging in repetitive high intensity interaction with dominant lizards and to accrue benefits from such avoidance of high intensity interaction.

The benefits that could accrue from avoiding unnecessarily high intensity are several. One obvious benefit is energy savings from not engaging in high intensity interaction. Less energy would be expended to define the relationship between two male lizards at that time. Interaction could end when the subordinate recognizes the dominant and energy that would have been utilized in dispaying is saved for use in other activity.

Another benefit could be reduced susceptibility to predation. When a lizard is engaged in high intensity interaction its attention is focused on the other lizard; and, the display behavior involved renders the lizards highly conspicuous. This situation could allow a predator to more readily locate the lizards and to approach them more easily without detection.

A further benefit could be reduced possibility of injury. Since A. lividus males do engage in potentially injurious behavior, jaw-fencing, the deleterious effects of injury could be avoided if the possibiltiy of injury is reduced. Individual recognition could allow cessation of interaction before jaw-fencing occurred.

The significance of individual recognition therefore is that individual lizards recognizing other individuals with which a dominance relationship has been previously established could interact in a manner which causes benefits to accrue to the lizards involved. However, there are some important assumptions present. One assumption, probably most important, is that A. lividus males do recognize other lizards with which a dominance relationship is established. The second assumption, which relies on the first, is that when a lizard does recognize other individuals, it will act in a manner which would garner the benefits outlined above. Both of these assumptions remain to be proven.

The relationship between duration of the downward motion and position within a display is difficult to interpret. The increased duration of the downward motion as a display is performed later in a volley may be accountable via a fatigue factor; the effectors involved in the performance of the display become fatigued during repetitive performances of the display.

The type B display is highly unstereotyped. This display consists of a sequence of similar bobs produced by movement of the head and forelegs. The statistical analysis of the display indicates a reduction of the interbob pause during the performance of the display. The high degree of variability in this display may allow it to function as a signal about internal motivational state of the performing lizard; but this is unclear. There does not appear to be an analogous situation with the signature display in which lizards performed individually specific displays. The type B display appears to be very similar to the display behavior of A. opalinus which possesses little or no stereotypy (Jenssen, 1979).

It was noted that the type B display also appeared to function as a courtship display. In _A. lividus_, species specific courtship displays and aggressive displays would not be required to differ in order to broadcast information with regard to species and gender. As other anoline species are not present, there would not be a need for additional display types to broadcast information as to the species of the individual. Being a highly dimorphic lizard, information with regard to gender is implicit in the individual's morphology.

The relationship between intra-volley pause and the four variables it was correlated against was not significant. This would indicate that IVP is independent of the displays which appear prior to or following the pause. The positive correlation of mean IVP with displays per volley which was significant is difficult to interpret in light of the previous statement. It would appear that as more displays are given in a volley, the mean IVP becomes larger. Fatigue may be a factor involved in this, since the more a lizard displays, the longer the effectors will need rest in order to display as vigorously. The positive correlation of IVP and position within volley also supports this.

The negative correlation of mean bobs per display with displays per volley may also be interpreted as support for a fatigue factor involved in the type B display. By bobbing less frequently per display when performing more displays the lizard may be effectively preventing over fatigue of the effectors involved. As other, more strenuous behavior may occur during an interaction between two males, the lizards could be preserving their energy for later.

The behavior which male A. lividus perform during inter-male interactions seems to be a means of communicating relative motivational state and social status. The display repertoire is not very large; but, the displays observed each appear to represent a higher level of intensity. Signature display and dewlapping would be the lowest intensity interaction; and jaw-fencing would be the highest. Type B display and sway display represent intermediate levels, sway probably being performed generally during higher intensity interactions. The information content of the displays could be such that the individuals involved in an interaction would be able to assess information relative to its opponent and alter its behavior accordingly.

The interaction behavior observed in this study may bear some significance for anoles other than A. lividus. Behavior is a character of a species much as another character subject to environmental and genetic control. There is evidence that anoline social display behavior is under genetic control (Jenssen, 1977c). There have been several studies of anoles using display behavior as a taxonomic character; and, these studies have, in general, confirmed presumed taxonomic relationships (Echelle et al. 1971; Gorman, 1968; and

Ruibal, 1967).

This study represents the first investigation of the social behavior of Anolis lizards within the bimaculatus series. The need for continued research into this subgroup of the genus Anolis is warranted by the unique conditions of the existence of these lizards, the so-called "natural laboratory". A comparative study of the social behavior of the bimaculatus series could yield much information with regard to the many and sundry influences on the evolution of social behavior.

CONCLUSIONS

Anolis lividus possesses two distinct head-bobing displays. One display, type A, is simple, highly stereotyped, and believed to be the signature display. The other head-bobbing display possesses a variable number of similar head bobs with a trend toward shortening the interbob pause as a display continues. An unusual rocking motion display named sway behavior may occur during male interactions. The observed male interaction behaviors allow for progressive intensification of an interaction through the use of the different behaviors according to a heirarchy of increasing intensity.

APPENDIX 1

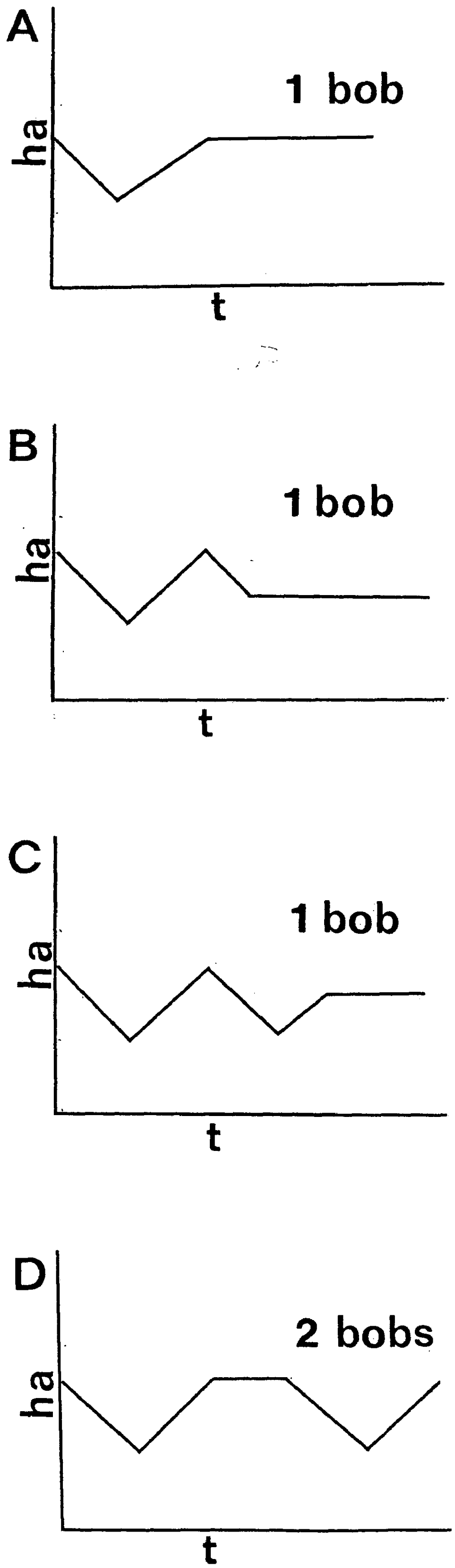
RAW DATA FOR THE SIGNATURE DISPLAY

Below is recorded the raw data of the length of the downward motion for the Signature display. The lizards identification number is recorded and next to the identification number is the volley number in which the displays were present. Following the volley number in sequential order from right to left are the individual measurements for each display in the volley. Note that some lizards possess only one volley.

LIZARD NO.	VOLLEY NO.	INDIVIDUAL MEASUREMENTS
0011	1	9,12,13
0011	2	10,10
0210	1	8,12
0210	2	14,14,12
0210	3	3,7
1030	1	7,9,10,12,13,14
1100	1	7,9
1100	2	7,7,8,9,10,10,10,11,11
1100	3	9,9,10,12,13,14
2030	1	7,8,11
2100	1	3,3,2,3,3,3
4041	1	5,6,6,7
4041	2	4,5,5
4041	3	6,6,7

APPENDIX 2 SAMPLE ANALYSIS

On the following page are several representations of bobs encountered during the analysis of films of the Type B display. On each graph the number of bobs as they would have been scored during analysis is written. Time is abbreviated t and head amplitude is abbreviated ha. Graphs A through C would each have been scored as one bob. Graph D is scored as two bobs because of the distinct pause between the two downward movements.


A
1 bob
ha
t
B
1 bob
ha
t
C
1 bob
ha
t
D
2 bobs
ha
t

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