

**DESCRIPTIVE ANALYSIS AND SOCIAL
CORRELATES OF AGONISTIC DISPLAYS OF
ANOLIS LIMIFRONS (SAURIA, IGUANIDAE)**

by

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(With 12 Figures)
(Acc. 25-V-1975)

INTRODUCTION

Displays in iguanid lizards consist of vertical movements by some part of the body which effect a change in head amplitude; this can take place by moving only the head and neck, or push-ups may be performed by alternate extension and flexion of the front legs, or all four legs may be employed in the push-ups. These types of body movements may be combined with such possible modifiers as erection of nuchal crest, gorged throat, lateral body compression, tongue protrusion, color changes, or tail movements. The addition of postures and certain movements to the basic head bobbing pattern presumably modify the display's signal value. In anoline species, displays are further augmented by the ability to extend a distinctly colored dewlap.

To date most published reports of agonistic iguanid display behavior have described each species or population as being characterized by a single unique display pattern (BLANC & CARPENTER, 1969; BUSSJAEGER, 1971; CARPENTER, 1961a, 1962a, b, 1963, 1966a, 1967a; CLARK, 1965; ECHELLE, ECHELLE & FITCH, 1971b; FERGUSON, 1971, 1973; LYNN, 1965; MCKINNEY, 1971). The species unique pattern has been subdivided into two quasi-functional categories: (1) termed the "assertion" display if the head bob pattern is

1) We are grateful to C. C. CARPENTER, G. FERGUSON, A. S. RAND, J. STAMPS, and E. E. WILLIAMS for their criticism of the manuscript, as well as for the courtesy and assistance extended to us by Dr RAND and the Smithsonian Tropical Research Institute staff during our stay in Panama. The project was supported by grants to T.A.J. from the National Geographic Society (NGS No. 1033) and National Science Foundation (NSF P4B3009-000). Certain STRI employees and facilities contributing to the study were also supported by the National Science Foundation (grant B 01901X to Dr Ernest E. WILLIAMS).

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performed with no or few modifying postures and appears during low-keyed social conditions (*e.g.*, after perch site relocation), and (2) called the "challenge" display if the pattern is performed with exaggerated vertical head movement, is accompanied by modifiers, and occurs during strong agonistic social contexts (*e.g.*, male-male encounters). Though the displays are susceptible to some individual variation and the assertion display may at times contain fewer units than the corresponding challenge display, the displays of these two categories, nevertheless, are described as sharing the same head bob pattern for a given species. This "assertion-challenge" display type is reviewed by CARPENTER (1967b: 87-88) and BUSSJAEGER (1971: 35-36).

Though the agonistic display repertoire of many iguanids may be adequately characterized by a single, species-typical "assertion-challenge" pattern, recent evidence indicates that some members of the genus *Anolis* exhibit multiple display repertoires. STAMPS & BARLOW (1973) report a complex of display patterns in *Anolis aeneus* which is not easily fit into the assertion-challenge mold. JENSSEN & ROTHBLUM (unpubl. data) found four agonistic display patterns performed by male *Anolis townsendi*. Ongoing studies by JENSSEN have uncovered extensive repertoires in *Anolis opalinus*, *Anolis grahami*, and *Anolis brevirostris* (unpubl. data). In *Phenacosaurus heterodermus*, a member of one of the "anole" genera, there are two distinct agonistic display patterns (JENSSEN, 1975).

This paper presents the entire agonistic display repertoire of male *Anolis limifrons*. However, a detailed description of the species' signature display (the *A* display), which is nearest in function to the assertive category of non-anoline iguanid displays, appears elsewhere (JENSSEN & HOVER, 1976).

During this research we have addressed ourselves to the following questions:

- 1) How many display types can males perform?
- 2) How much variation is there in the performance of each display type?
- 3) Is the variation random or can it be related to other aspects of display performance or to social factors?
- 4) What are the contextual (social) factors important in the appearance of each display type?
- 5) How do displays of one lizard relate to the subsequent behavior of lizards observing the displays?

MATERIALS AND METHODS

We conducted this research over a two year period from June, 1972 to May, 1974, and employed 666 filmed displays from 23 lizards in our analysis.

All subjects were collected in the Canal Zone, Panama. Details of the collection and

maintenance of *A. limifrons* have been presented elsewhere (JENSSEN & HOVER, 1976).

Filming and film analysis.

Males were filmed in 1.2 m (L) \times 0.6 m (W) \times 0.6 m (H) enclosures with tropical forest habitat simulated by using tree stumps, branches, and plastic vegetation. In the photo enclosures there were varying combinations of 1-3 males with 3-5 resident females. Filmed sequences were taken with a Nizo S80 Super 8 camera, using a film speed of 18 frames/s, and loaded with Kodachrome II film. Two quartz iodine floodlights (Colortran Quartz-King 500) fitted with heat filters provided the light. Techniques for the frame-by-frame analysis of the resulting films are detailed elsewhere (JENSSEN & HOVER, 1976).

Displaying males were filmed in three contexts:

- 1) With no other animals apparently visible to the resident male and thus no lateral presentation toward a conspecific,
- 2) While orienting laterally toward females,
- 3) Extended interactions with introduced dominant males.

From the resulting displays, five major display types (*A-E*) were recognized on the basis of body parts moved, pattern of head movement, and time of appearance of the dewlap. Statistical comparisons were made within and between display types using data pooled from a number of individuals. Mean, standard error of the mean, and 95% confidence limits of the mean were computed for number of head bobs, total duration of the first seven head bobs, and duration of each of the first seven head bobs for each display type. In addition to a strictly temporal analysis, display patterns were further quantified by converting the duration of each of the first seven head bobs to a percentage of the total duration of the first seven head bobs. This was done to study whether head bob proportionment varied between displays. Percentages were submitted to arcsine transformation before statistical comparison.

Partition experiments.

It was often impractical to record contextual data during filming; therefore, partition tests were run to more accurately correlate contexts during which various display types appeared. An enclosure 2.4 m (l) \times 0.6 m (h) \times 0.8 m (w) at the top and 0.6 m (w) at the bottom was divided into halves by an opaque, removable partition (Fig. 1). The glass front of the cage was slanted to reduce the possibility that an animal inside the cage would see its own reflection. The simulated forest habitat in the two halves of the enclosure was in mirror image. This was done by replicating the configuration, color, and position of each habitat element of one half of the cage in the other half. The major perching substrates were matched by using the split halves of stumps and adjacent sections cut from common limbs. Various forms of plastic plants allowed precise duplication and positioning of vegetation between the two habitats. Each major feature of the habitat was assigned a number. A tape along the bottom front edge of the cage was marked in 10 cm increments beginning with zero at the partition and proceeding toward each end; this located the position of any animal in the cage and allowed calculation of distance between animals.

With the partition in place a dominant male was placed in each half of the cage along with a resident female. These two males had previously been held in separate cages, and thus had never had or at least had no recent contact with each other. Animals were allowed to remain in the cage 24 hr before trials were begun. To ensure agonistic interaction, an attempt was made to avoid a large size disparity between males, since previous observations in the holding cages had indicated that small males tend to avoid much larger males by hiding in the foliage.

Five trials at 24 hr intervals were run on each of six pairs of males. The animals were observed for one hour with the partition in place, then for one hour after removing the partition. Observations were tape recorded and included all changes of position by

males and females, display types performed, and other behavior such as feeding, drinking, defecation, and shedding. The position of the lizards and elapsed time since the initiation of observations were recorded for each behavior. Observed displays were assigned to one of the five major display types.

Walk-in cage observations.

During August, 1973, over 36 hr of observations were made on 12 male and five female *A. limifrons* in a large outdoor cage at the Smithsonian Tropical Research Institute (STRI) in Balboa, Panama Canal Zone. The screen cage measured 4.9 m (l) \times 2.9 m (w) \times 2.4 m (h). The interior was supplied with seven clumps of branches, bricks, and plants. The top and sides of the cage were partially covered by vines.

Observations were made by sitting quietly in one corner of the cage and taking written notes on *A. limifrons* individuals. Animals had previously been toe clipped for permanent identification and given paint marks to allow individual recognition at a

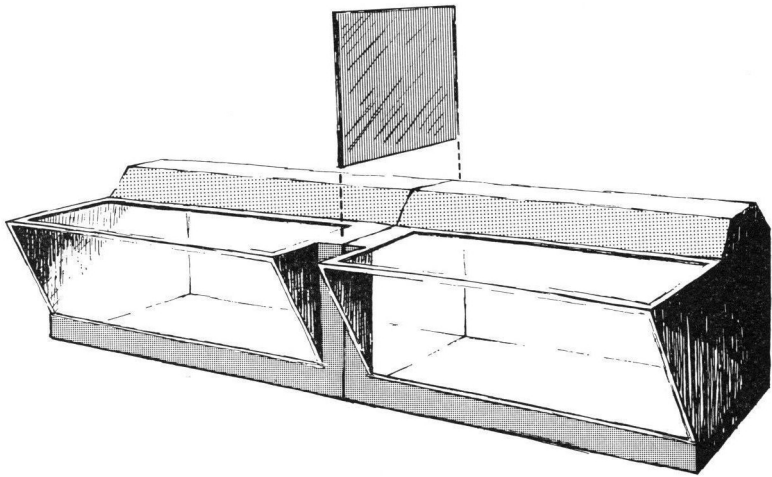


Fig. 1. Enclosure used in partition experiments.

distance. Habitat clumps and some of the larger features of each clump were assigned numbers to facilitate recording of position and movement. Observations were made on as many overt behaviors as possible. Displays were assigned to one of the five major display categories. Where possible the social context of the display was noted.

RESULTS

Film analysis.

Filmed displays were divided into five major types, designated *A*, *B*, *C*, *D* and *E*, on the basis of head bob pattern, time of throat fan appearance, and body parts moved. A sixth display type, dewlapping, consisted of a single extension of the dewlap without head bobbing, and was not analyzed. Only 20 displays of this last type were filmed, and the duration of fan extension was extremely variable.

Display type A. The type *A* display was the most frequently performed

display, consisting of a variable number of head bobs, the first five of which were performed in a fairly distinct *one long-three short-one long* pattern (Fig. 2). The dewlap begins extension before the first head bob and remains extended throughout the display. A detailed analysis of this display type has been made elsewhere (JENSEN & HOVER, 1976).

Display type B. The *B* display has a pattern similar to type *A*, but is distinguishable because the dewlap appears later in the display (Fig. 2). As in the *A* display, the head amplitude pattern is generated primarily by movement of the head and neck; occasionally the forebody is gradually raised during display by the slow extension of the front legs.

Five display varieties are subsumed under the type *B* designation because dewlap extension may begin during any of the first five head bobs (*B*₁ displays have dewlap extension on the first head bob, *B*₂ displays have

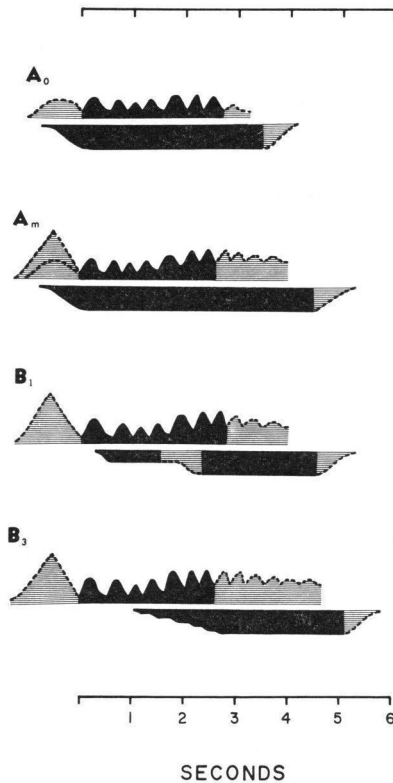


Fig. 2. Generalized DAP graph of male *Anolis limifrons* display types *A* and *B*. Grey areas indicate display components not always present. Upper block of each figure indicates head amplitude through time, and lower block shows dewlap extension through time.

dewlap extension on the second, *etc.*). Associated with an increasingly delayed dewlap appearance is an increased number of total head bobs for *B* displays (Fig. 3).

B displays were sometimes performed in volleys of from two to four displays at a time, similar to the volleys of type *A* displays (JENSSEN &

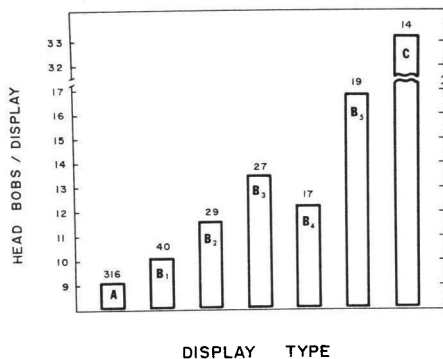


Fig. 3. Number of head bobs versus display type. Subscripts in type *B* displays refer to the head bob in which the dewlap first appears. Numbers over bars give sample sizes.

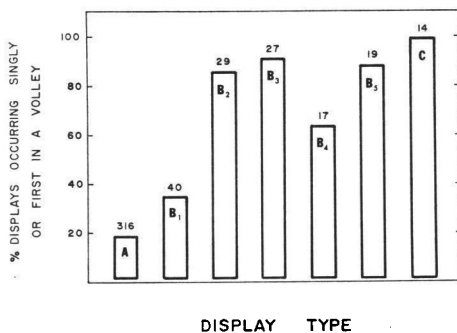


Fig. 4. Percentage of displays occurring singly or first in a volley versus display type. See additional notations of Fig. 3.

HOVER, 1976). Of the *B* displays, *B*₁ variant was least likely to be given singly or first in a volley of displays (Fig. 4).

Display type C. In the type *C* display, the *one long-three short-one long* head bob pattern characteristic of type *A* and *B* displays is absent (Fig. 5). In addition the dewlap appears during the sixth head bob or later. The display pattern is again produced primarily by head and neck movement, though the front legs are always gradually extended during the display.

The first seven head bobs of the *C* display were performed significantly faster than those of the other display types (Student-Newman-Keuls multiple

range test after single classification analysis of variance, $F = 20.832$; $df = 15, 677$; $p < 0.05$; Fig. 6). The duration of the fifth bob is shorter in *C* displays than in *A* and *B* displays (Fig. 7).

Fourteen type *C* displays were filmed. However, many more of this distinctive display type were seen during unfiled encounters (*i.e.*, partition experiments). With display type *A* and the five varieties of type *B*, the *C* display forms a display series characterized by increasing numbers of head

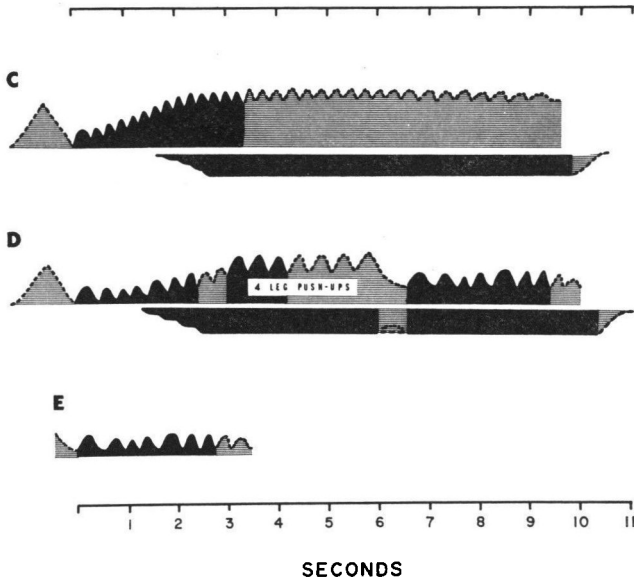


Fig. 5. Generalized DAP graphs of male *Anolis limifrons* display types *C*, *D*, and *E*. See additional notations of Fig. 2.

bobs, progressively later appearance of the throat fan during display, and eventual loss of the *one-three-one* bob pattern (Fig. 3 and 7).

Display type D. The type *D* display begins with head bobs performed with the type *B* pattern, followed immediately by a series of alternate extension and flexion of all four legs (4-legged push-ups). The push-ups are followed, in turn, by another series of head bobs having the type *A* pattern (Fig. 5). With the exception of the 4-legged push-ups, the movement of the head and neck produced the amplitude pattern for the *D* displays.

The 29 filmed type *D* displays were performed by eight males. The initial portion of the display consisted of seven to 20 head bobs (mean of 8.9 ± 0.48), followed by two to eleven push-ups (mean of 7.1 ± 0.49) and eight to 12 more head bobs (mean of 9.6 ± 0.21). Initial appearance of the throat

fan varied from before the first head bob to the eighth bob (mean of 3.8 ± 0.35).

Display type E. The final major display type consists of the type *A* pattern performed by alternate extension and flexion of the front legs rather than head and neck motion (Fig. 5). The neck is held rigid and the fore part of the body is curved in a characteristic manner, hereafter designated the "S" posture (Fig. 8). The dewlap does not extend or does so only to a limited extent late in the display.

Type *E* displays, like display types *A* and *B*, were often performed in volleys. Displays performed singly or first in a volley had a greater mean number of head bobs and shorter mean duration for the first seven head bobs than those displays appearing second or third in a volley (Fig. 9 and 10).

Each of the five display types was sometimes augmented by certain postures (static modifiers) or movements (dynamic modifiers) (Table 1). The same display modifiers can occur with different display types or can be

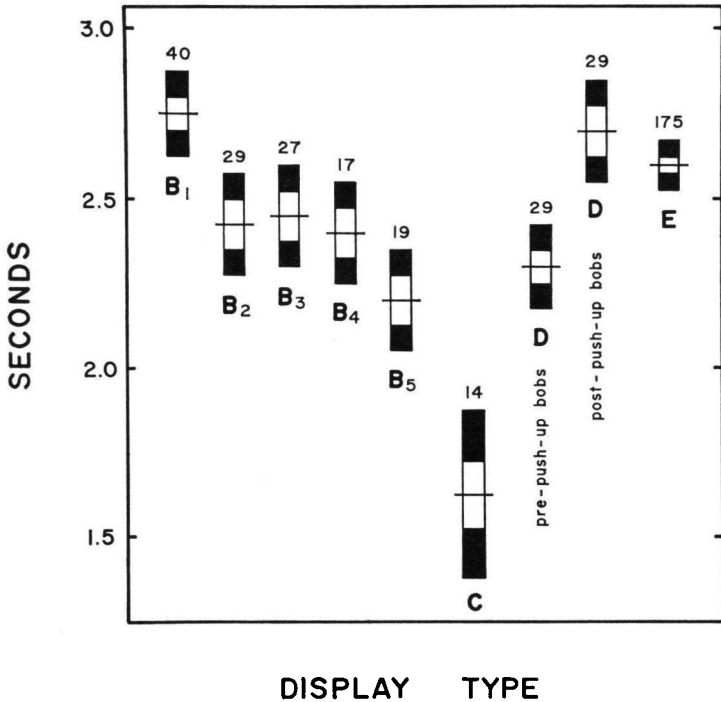


Fig. 6. Duration of the first seven head bobs versus display type. Horizontal line indicates mean duration, outer ends of white bars indicate standard error of the mean, and outer ends of black bars are 95% confidence limits of the mean. Numbers over bars provide sample sizes.

performed independently (the "postural" displays of RAND, 1967), and were thus not considered as criteria for distinguishing different display types. A more complete discussion of the term, "display modifier," and a list of modifiers frequently observed in *A. limifrons* has been presented by JENSSEN & HOVER (1976).

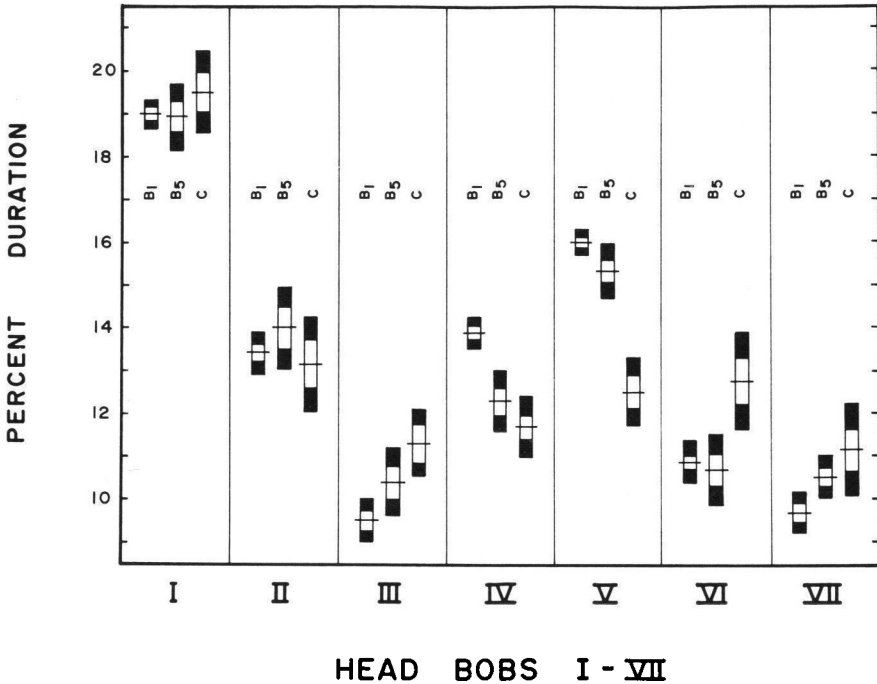


Fig. 7. Percent duration of each of the first seven head bobs of display types, B_1 , B_5 , and C . Statistical notation as in Fig. 6.

Partition experiments.

With the exception of dewlap extension without head bobbing, all display types observed in the partition tests occurred more frequently after removal of the partition than with the partition in place (Fig. 11). Only the dewlap display and display type A occurred commonly with the partition in place, and were either directed toward the female present or were performed as "assertive" display (*sensu* CARPENTER, 1967b) without orientation toward another individual. The few type D and E displays observed before removing the partition were performed during two different trials when the lizard was within a few cm of the front glass. These were the only instances in the tests where obvious reactions to the lizard's own reflection from the enclosure's glass front occurred; the slanted glass front eliminated reflection into the

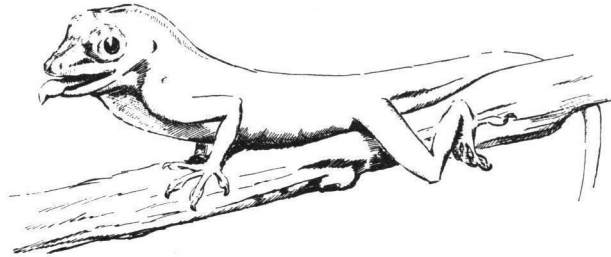


Fig. 8. The "S" posture assumed by male *Anolis limifrons* during performance of type E displays.

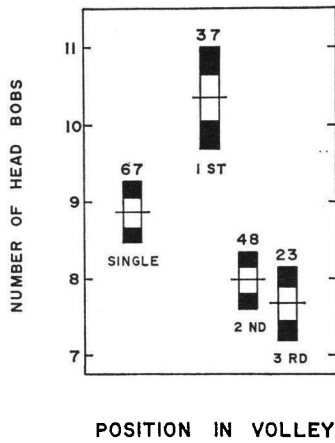


Fig. 9. Number of head bobs versus position in a display volley for type E displays. Statistical notations as in Fig. 6.

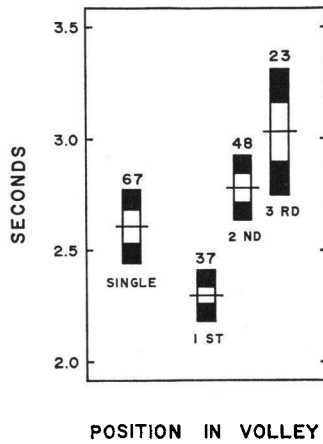


Fig. 10. Duration in seconds of the first seven head bobs versus position in a display volley for type E displays. Statistical notations as in Fig. 6.

interior except at very close range. The same two males continued to perform type *E* displays toward their reflections for short periods after removal of the partition (dotted lines in Fig. 12).

The type of displays appearing after removal of the partition were related to distance between males (Fig. 12). Only displays occurring singly or first in a display volley were included in this analysis because display occurring later in a volley were almost invariably type *A*.

Volleys beginning with type *A* displays appeared most frequently when

TABLE 1

Frequencies of occurrence (Freq.) and percent occurrence (%) of some display modifiers accompanying the display types of Anolis limifrons

Display types and sample size (n)	Raised nuchal crest		Mouth open w or w/o tongue protruded		Exaggerated head roll	
	Freq.	%	Freq.	%	Freq.	%
<i>A</i> (316)	197	62	84	27	28	8
<i>B</i> ₁ - <i>B</i> ₅ (132)	124	94	82	62	39	29
<i>B</i> ₁ (40)	39	98	26	65	9	23
<i>B</i> ₂ (29)	26	90	11	38	7	24
<i>B</i> ₃ (27)	25	93	20	74	12	44
<i>B</i> ₄ (17)	15	88	10	59	1	6
<i>B</i> ₅ (19)	19	100	15	79	10	53
<i>C</i> (14)	14	100	10	71	9	64
<i>D</i> (29)	29	100	28	97	26	90
<i>E</i> (175)	175	100	149	85	1	< 1

males were separated by nearly the entire length of the cage (Fig. 12). As one or both males approached the boundary between cage halves, display types *B* and *C* appeared. Volleys beginning with types *B* or *C* often alternated with type *A* initiated volleys.

The type *D* display occurred only at relatively close range (Fig. 12), and in all cases immediately preceded or followed a quick approach by one or both males. The type *D* display was invariably followed by type *E* volleys.

Display volleys beginning with the type *E* pattern generally included only type *E* displays. These displays were performed at close range (Fig. 12) with the participants positioned similar to the "face off" position reported by CARPENTER (1967b), where animals oriented laterally to each other with the head of one toward the tail of the other. In one instance several type *E* volleys immediately preceded a fight and the eventual flight by one of the combatants.

At any point after the initiation of an encounter (display exchange), both males were generally performing the same display type. Thus in 61%

of the 83 instances where the display of one male was followed within one minute by a display from the opponent male, the display of both males were of the same type (Table 2). This relationship was especially strong for the type *E* display (92%). If both males were actively displaying, the type *E* display was virtually the only display performed at inter-male distances closer than 10 cm. In general, when a male responded to an opponent's display with a different display type, it was usually a type higher in the $A \rightarrow B \rightarrow C \rightarrow D \rightarrow E$ series.

Several observations indicate that males did indeed react to the behavior

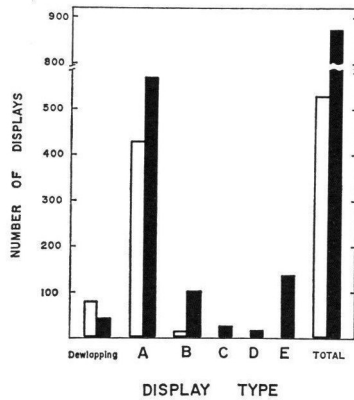


Fig. 11. Frequency of performance of each display type before (white bars) and after (black bars) removal of partition in partition experiments.

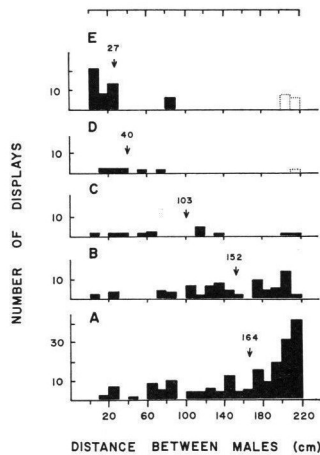


Fig. 12. Frequency of performance of each display type versus distance between males in partition experiments. Only displays performed singly or first in a volley were considered. Arrows indicate sample means.

of the opponent male, rather than merely reacting to the presence of a male at a certain distance. Those encounters during which only one male displayed were found to be devoid of *C*, *D*, or *E* display types, even though the males were occasionally within a very few centimeters of each other. In such cases, the non-displaying male held his body flattened against the substrate, while the displaying male performed type *A* or type *B* displays. Such instances are in fact responsible for all *A* or *B* initiated volleys recorded at close distance (Fig. 12).

TABLE 2

Type of single or first in a volley displays performed by a male during the partition experiments which were in response to the display type given just previously (< 1 min) by another male

Display type of first male	Display type of second male		
	Same type	Higher type	Lower type
Dewlapping	0	1	0
<i>A</i>	9 (39%)	14 (61%)	0
<i>B</i>	19 (71%)	3 (12%)	4 (17%)
<i>C</i>	1	2	3
<i>D</i>	2	3	0
<i>E</i>	22 (92%)	0	2 (8%)
All types	51 (61%)	23 (28%)	9 (11%)

"Higher" and "lower" refer to the display types of the series, Dewlapping $\rightarrow A \rightarrow B \rightarrow C \rightarrow D \rightarrow E$, where dewlapping and *A* are low and *E* is high.

In one encounter two males performed several type *E* volleys at a range of about 10 cm. One male (male L) eventually turned and moved approximately 15 cm away from the opponent (male R). As male L moved, male R began a type *D* display. When male R began the four-legged push-up portion of the display, male L immediately began to perform four-legged push-ups *without* first performing the initial head bobs characteristic of the *D* display. This was the only time a male was observed to perform four-legged push-ups without the preceding head bobs.

Walk-in cage observations.

Activity in the outdoor cage generally centered around the seven habitat clumps. Each clump was separated from the other clumps by a distance of at least one meter. Only one actively displaying male occupied any given habitat at one time, and most males confined their activities to a single clump. One male, however, freely moved through three clumps and displayed at or chased other males in these clumps.

During the 36 hr of observation, a total of 372 type *A* displays, 51 type *B* displays, 19 type *E* displays, 15 dewlap-only displays, and five type *C* displays were seen. No type *D* displays were observed. Although the social context of display could not always be determined, no contradictions with the results of the partition tests occurred. Type *A* and *B* displays were performed in relatively long distance interactions between males (>0.5 m). Many *A* displays were performed without obvious orientation toward other individuals, generally before or after a change of position by the displaying male. Type *E* displays were seen only in close range interactions between males.

Most interactions between males were brief, ending with retreat by one or the other individual. No ritualized jaw sparring was ever observed, either in the walk-in cage, during the partition experiment, or during filming sessions. Each habitat clump was occupied by a single male, designated the resident, that was dominant to all other individuals entering that clump.

A typical example follows:

11:24. Male 11 moves into clump T-3, onto forked log, head down.

11:29. Male 11 moves to the small log in T-3, and is now visible to resident male 5. Male 5 turns lateral to male 11 and performs a type *B* display (10 bobs), followed immediately by an *A* display (8 bobs). The males are approximately 0.5 m apart.

11:30. Male 5 moves toward male 11. Male 11 moves out of clump T-3.

In one instance a male was released at the edge of a clump occupied by a resident male:

13:45. Male 10 released into clump T-3. Resident (male 5) is on a cement block, head down.

13:48. Male 10 moves toward male 5 to within 1 m. Male 5 orients laterally to male 10 and performs a *B* display (15 bobs), followed by an *A* display (9 bobs).

13:52. Male 5 performs a *B* display (11 bobs), followed by an *A* display (9 bobs).

13:53. Male 5 performs a *B* display (10 bobs), still lateral to male 10.

13:54. Male 10 performs a *B* display (10 bobs). Male 5 immediately performs a *B* display (11 bobs), followed by an *A* display (8 bobs). The male 5 moves 5 moves to within 30 cm of male 10 and performs an *E* display (9 bobs).

13:56. Male 5 performs type *E* (10 bobs), followed by *E* (8 bobs), *E* (7 bobs).

13:57. Male 5 performs *E* (10 bobs), then *E* (9 bobs), and *E* (8 bobs).

13:58. Male 5 performs *E* (13 bobs), then *E* (7 bobs), and *E* (7 bobs). Male 5 then jumps to within 10 cm of male 10 and assumes the "S" posture with tongue protruded. Male 10 flattens against substrate.

14:02. Male 5 performs a type *C* display, then licks substrate.

14:07. Male 10 shifts position slightly, male 5 immediately performs a *C* display, followed by an *A* (8 bobs). Male 10 moves away to about 0.5 m.

14:11. Male 5 performs a *B* display (15 bobs). Male 10 moves into foliage and out of sight.

Resident males in adjacent clumps did not direct displays at each other, although they were often in visual contact. Such males frequently performed *A* displays, but did not orient laterally toward other individuals.

DISCUSSION

Since CARPENTER (1961a, 1961b) introduced the concept of a single species-specific display pattern which can be performed without modifiers (assertion form) or with exaggerated amplitude and accompanied by modifiers (challenge form), nearly all published reports of iguanid behavior have presented a single agonistic display pattern for each studied species. Clearly, this framework is inadequate for *A. limifrons* and certain other anoles (STAMPS, 1973; STAMPS & BARLOW, 1973).

The results of the partition tests suggest that the display types of *A. limifrons* can be ranked in a manner which reflects an increasing aggressive level. Type *A* displays occur both in an assertion context (before removal of partition) and in long range interactions between males. As interactions progress and inter-male distance decreases, the other display types appear in the general order *B*, *C*, *D*, and finally *E* in close range interactions. The type *E* display, in fact, occurs in the face off position described by CARPENTER (1967b) for the challenge display of other iguanids.

Based strictly on display form, the *A* display could be interpreted as being the initial pattern of an *A* through B_5 display type continuum. However, there seems to be a basic functional distinction between the *A* and *B* display types. In the partition experiments, almost no *B* displays were performed during the male-female social context (partition in place); in contrast, *B* displays were performed frequently within the male-male context (partition removed). This observation and the fact that the *A* display appeared eight times more frequently than the most common *B* display variant lead us to recognize the two displays as a natural rather than artificial division.

Interestingly, certain characteristics of the display types change in a systematic way corresponding to the $A \rightarrow B \rightarrow C \rightarrow D \rightarrow E$ series. These include the following:

1) The total number of head bobs per display increases in the series $A \rightarrow B \rightarrow C$.

2) The initial appearance of the dewlap is more and more delayed in the series $A \rightarrow B \rightarrow C$, and the dewlap does not appear at all in most type *E* displays. Within the *B* display type the series $B_1 \rightarrow B_5$ is characterized by an increasingly late dewlap appearance correlated with an increasing number of head bobs (Fig. 3).

3) There is a trend for certain display modifiers to appear with greater frequencies in the series $A \rightarrow B \rightarrow C \rightarrow D \rightarrow E$ (Table 1). An erected nuchal crest, for example, was present in 67% of filmed type *A* displays, 88 - 100% of the type *B* varieties, and 100% of the type *C*, *D* and *E* displays. A similar trend exists for tongue protrusion and a large-amplitude introduc-

tory movement, "Exaggerated Roll" (see JENSSEN & HOVER, 1976, for definitions). However, type *E* displays, which lack significant dewlap extension, are rarely preceded by Exaggerated Rolls; perhaps this is because dewlap elaboration would not be advantageous since combatants are juxtapositioned and physical contact is imminent.

4) Display types *A*, *B*, and *C* are performed primarily by head and neck motion. Type *D* includes head and neck motion, and also adds a series of four-legged push-ups. Type *E* is performed only by front leg push-ups and is augmented by the "S" posture.

5) The likelihood that a particular display type will occur as a second or third display in a display volley decreases with the series $A \rightarrow B \rightarrow C \rightarrow D$. Type *A* displays are normally positioned second or third in volleys initiated by *A*, *B*, *C*, or *D* displays. Type *B* displays were occasionally seen as following displays in *B* or *C* initiated volleys, but never in type *A* initiated volleys. A single type *C* display was observed as a following display in a *C* initiated volley. Type *D* displays never occurred as a following display volley. Type *E* displays did occur as following displays, but only in *E* initiated volleys.

Within the ranked display series are mechanisms which allow a further refinement in display performance. A single display type, for example the type *A* display, can vary in total number of head bobs performed. This variation, however, is not random but can be related to the position of the display in a display volley or to the presence or absence of display modifiers (JENSSEN & HOVER, 1976). In volleys having only *A*, *B*, or *E* displays, the initial display had the most head bobs (pure *C* and *D* display volleys were not generally performed). If modifiers are present, the number and type probably influence the information content of the display.

The total effect, then, is a display repertoire made up of a graded series of display types, each type apparently reflecting a more strongly motivated agonistic state than the type immediately preceding it in the series. Within display types a similar graded series is possible based upon certain aspects of display variability (*e.g.*, number of added bobs, number of other dynamic and static modifiers).

Obviously, the display behavior of anoles which exhibit repertoires as complex in structure, and presumably in information content, as that of *A. limifrons* cannot be understood without considerable attention. ECHELLE, ECHELLE & FITCH (1971a), for example, reported only a single aggressive display type for *A. limifrons*, apparently the type *C* display described here. Other authors (*e.g.*, RUIBAL, 1967) have despaired over the overwhelming lack of stereotypy in the display of certain anoles. It is entirely possible that

this seeming lack of stereotypy is in reality a reflection of the widely accepted notion that iguanid lizards can assert and challenge with only a restricted display repertoire, and that anything that looks more complex than this is random variation.

Anoline lizards deserve close examination in any consideration of the ecology and evolution of lizard social behavior. The data reported here should provide a basis for future comparisons with other anoles, and we suggest several lines of inquiry:

1) The enumeration of contextual factors related to display performance only indirectly approaches the problem of display function. Experimental methods are needed to clarify more precisely what information is being conveyed by each display type and what parts of the display are most important in this function.

2) Ideally, each display type should be recorded under natural conditions. Descriptions of display behavior should be put in the context of the natural social environment of the species. In eliciting these displays, techniques should be cautiously tested. Using a mirror or a tethered lizard dropped into another's territory to elicit displaying can at times distort the unfolding of the natural sequence of the display repertoire (MILSTEAD, 1970: 351; pers. observ.).

3) The large repertoire of at least a few anoles raises questions on the ecological and evolutionary significance of repertoire size. Why, for example, do some anoles such as *Anolis nebulosus* have limited repertoires consisting of only two basic agonistic display patterns (JENSSEN, 1970, 1971), while others have much larger repertoires? Though several possibilities suggest themselves (*e.g.*, type of social organization, number of syntopic congeners, seasonal versus nonseasonal breeding, kind and intensity of predation, structural makeup of the habitat), little data for judging the importance of any of these factors exist. Essential to clarifying the factors determining repertoire size are studies of a purely descriptive nature. A comparative approach is most profitable when studies are based on a thorough knowledge of the range of possible behaviors for each examined species.

SUMMARY

Analysis of 666 filmed displays of 23 male *Anolis limifrons* from Panama revealed:

1) The species has an agonistic repertoire of five head bob patterns (*A-E*) and one dewlap display.

2) During male-male interactions, the decrease in intermale distance correlates with a progression of display usage from $A \rightarrow B \rightarrow C \rightarrow D \rightarrow E$.

3) When lizards exchanged displays within a short time span (1 min), the answering animal usually performed a display type of the same or the next type up in the $A \rightarrow E$ series, almost never was the answering type further down in the $A \rightarrow E$ series.

4) The *D* display is the most elaborate pattern and the *E* type the least; the *E* display occurred during face off orientations between combatants when they were within leaping distance of each other.

5) There was a trend for display modifiers to appear with greater frequency with the progression of display types from *A* to *E*.

6) Displays were frequently performed in volleys of two to four displays at a time, usually being three to a volley.

7) The first display of a volley was always of "higher" type in the display series $A \rightarrow E$ than the subsequent display of a volley *i.e.*, *B, A, A; C, B, A; D, A, A*; if all the displays of a volley were of the same type, the first contained more modifiers than the others (*e.g.*, introductory movements, more head bobs).

8) Presumably, the stepwise progression of display types from *A* to *E* during agonistic encounters reflects increase in motivational state.

REFERENCES

- BLANC, C. & CARPENTER, C. (1969). Studies on the Iguanidae of Madagascar III. Social and reproductive behavior of *Chalaradon madagascariensis*. — J. Herpetol. 3, p. 125-134.
- BUSSJAEGER, L. (1971). Phylogenetic significance of the comparative ethology of the *spinosus* ground of *Sceloporus* (Iguanidae). — Ph. D. Thesis, Univ. Oklahoma, Norman.
- CARPENTER, C. (1961a). Patterns of social behavior of Merriam's canyon lizard (*Sceloporus m. merriami*-Iguanidae). — Southwest. Natur. 6, 138-148.
- (1961b). Patterns and social behavior in the desert iguana, *Dipsosaurus dorsalis*. — Copeia 1961, p. 396-405.
- (1962a). Patterns of behavior in two Oklahoma lizards. — Amer. Midland natur. 67, p. 132-151.
- (1962b). A comparison of the patterns of display of *Urosaurus*, *Uta*, and *Streptosaurus*. — Herpetologica 18, p. 145-152.
- (1963). Patterns of behavior in three forms of the fringe-toed lizards (*Uma*-Iguanidae). — Copeia 1963, p. 406-412.
- (1966a). Comparative behavior of the Galapagos lava lizard (*Tropidurus*). — In: The Galapagos. Proceedings of the Galapagos International Scientific Project, R. BOWMAN (ed.), p. 269-273, Univ. California Press, Berkeley.
- (1966b). The marine iguana of the Galapagos Islands, its behavior and ecology. — Proc. California Acad. Sci. 34, p. 329-376.
- (1967a). Display patterns of the Mexican iguanid lizards of the genus *Uma*. — Herpetologica 23, p. 285-293.
- (1967b). Aggression and social structure in iguanid lizards. — In: Lizard ecology: A symposium, W. MILSTEAD (ed.), p. 87-105, Univ. Missouri Press, Columbia.
- CLARKE, R. (1965). An ethological study of the genera *Callisaurus*, *Cophosaurus*, and *Holbrookia*. — Emporia State Res. Stud. 13, p. 1-66.
- EHELLE, A., EHELLE, A. F. & FITCH, H. (1971a). A comparative analysis of aggressive display in nine species of Costa Rican *Anolis*. — Herpetologica 27, 271-288.
- (1971b). A new anole from Costa Rica. — Herpetologica 27, p. 354-362.
- FERGUSON, G. (1971). Variation and evolution of the push-up displays of the side-blotched lizard genus *Uta* (Iguanidae). — Syst. Zool. 20, p. 79-101.
- (1973). Character displacement of the push-up displays of two partially-sympatric species of the spiny lizards, *Sceloporus* (Sauria: Iguanidae). — Herpetologica 29, p. 281-284.
- JENSSEN, T. (1970). The ethoecology of *Anolis nebulosus* (Sauria, Iguanidae). — J. Herpetol. 4, p. 1-38.

- (1971). Display analysis of *Anolis nebulosus* (Sauria, Iguanidae). — *Copeia* 1971, p. 197-209.
- (1975). Display repertoire of a male *Phenacosaurus heterodermus* (Sauria: Iguanidae). — *Herpetologica* 31, In press.
- & HOVER, E. (1976). Display analysis of the signature display of *Anolis limifrons* (Sauria: Iguanidae). — *Behaviour*.
- LYNN, R. (1955). A comparative study of display behavior in *Phrynosoma* (Iguanidae). — *Southwest. Natur.* 10, p. 25-30.
- McKINNEY, C. (1971). Individual and intrapopulational variation in the push-up display of *Uta stansburiana*. — *Copeia* 1971, p. 159-160.
- MILSTEAD, W. (1970). Late summer behavior of the lizards *Sceloporus merriami* and *Urosaurus ornatus* in the field. — *Herpetologica* 26, p. 343-354.
- RAND, A. S. (1967). Ecology and social organization in the iguanid lizard *Anolis lineatopus*. — *Proc. U. S. Nat. Mus.* 122, p. 1-79.
- RUIBAL, R. (1967). Evolution and behavior in the West Indian anoles. — In: *Lizard ecology: A symposium*, W. MILSTEAD (ed.), p. 116-140, Univ. Missouri Press, Columbia.
- STAMPS, J. (1973). Displays and social organization in female *Anolis aeneus*. — *Copeia* 1973, p. 264-272.
- & BARLOW, G. (1973). Variation and stereotypy in the displays of *Anolis aeneus* (Sauria, Iguanidae). — *Behaviour* 48, p. 67-94.

ZUSAMMENFASSUNG

Eine Analyse von 666 gefilmten Imponierformen von 23 männlichen *Anolis limifrons* aus Panama zeigte folgendes:

- 1) Diese Gattung hat ein antagonistisches Repertoire von fünf Kopfnick- (*A-E*) und einem Kehlsackimponiergehaben.
- 2) Während Kontakten zwischen männlichen Tieren der *Anolis limifrons* ist die Verringerung des Abstandes korreliert mit einer Weiterschreitung der Imponierbenutzung von $A \rightarrow B \rightarrow C \rightarrow D \rightarrow E$.
- 3) Wenn Eidechsen Imponieren innerhalb einer kurzen Zeitspanne austauschen (1 Min.), vollführt das antwortende Tier meistens eine Imponierungsart des gleichen oder nächsten Typs in der $A \rightarrow E$ -Folge. Die Art der Antwort war fast nie weiter unten in der $A \rightarrow E$ -Reihe.
- 4) Das *D*-Imponiergehaben hat die überschwenglichste Form und die *E*-Art die geringste; das Imponieren fand während der Anfangsorientierung zwischen Streitenden statt, wenn sie innerhalb Sprungentfernung von einander waren.
- 5) Für Imponierungsabwandler zeigte sich eine Tendenz grösserer Häufigkeit in der Weiterschreitung des Imponierens, während die Typen sich von *A* zu *E* bewegten.
- 6) Imponieren erfolgte häufig in Serien von zwei bis vier Imponierarten auf einmal, meistens drei hintereinander.
- 7) Das erste Imponieren einer Serie war immer von der höheren Art in der Imponierfolge $A \rightarrow E$ als das folgende Imponieren der Reihe (z.B. *B, A, A; C, B, A; D, A, A*). Wenn das gesamte Imponieren einer Serie vom gleichen Typ war, enthielt das erste Imponiergehaben mehr Abwandler als alle anderen. (z.B. Einleitungsbewegungen, mehr Kopfnicken).
- 8) Wahrscheinlich spiegelt die schrittweise Fortführung des Imponiertyps von *A* bis *E* während eines antagonistischen Treffens eine Erhöhung des Motivierungsgrades wieder.