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DISPLAY ANALYSIS OF THE SIGNATURE DISPLAY OF *ANOLIS LIMIFRONS* (SAURIA: IGUANIDAE)

by

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(With 6 Figures)
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INTRODUCTION

Since CARPENTER & GRUBITZ (1961) introduced a graphic method for depicting lizard displays, many iguanid species have had their displays visually represented. However, an emphasis on quantification of lizard displays has been slow in developing. It is common for authors to mention observed variation in the displays, yet this variability is seldom measured and even more rarely incorporated into the display-action-pattern (DAP) graphs. With a few notable exceptions (FERGUSON, 1971, JENSSEN, 1971, 1975), there are no adequate statistical descriptions of saurian displays.

The importance of a more quantative approach may not have been recognized partly because of a long held assumption that lizard displays are very stereotyped species-specific behaviors relatively independent of experience. The fact that adult display behavior has been reported to appear shortly after hatching (CARPENTER, 1960, 1962; COOPER, 1971; JENSSEN, 1970: TINKLE, 1967), though not documented by film analysis, undoubtedly reinforced this conception.

However, work on *Uta stansburiana* (FERGUSON, 1971; MCKINNEY, 1971) and *Anolis nebulosus* (JENSSEN, 1971) showed marked interpopula-

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tional differences in these species' displays. Display duration of *A. nebulosus* displays could significantly vary with a lizard's age (JENSSEN, 1971). Recently BERRY (1974) noted consistent display differences between individual *Sauromalus obesus*; she suggests this interindividual display variability may function in individual recognition. *Anolis limifrons* has been found to possess a large display repertoire in which there are two display types of similar pattern (HOVER & JENSSEN, 1976). These findings emphasize the need to quantitatively characterize display types. Considerable data and careful analysis are needed to determine: (1) what behaviors are actually different display types in those species with large repertoires, (2) what behaviors are socially functioning variations of a single display type when that particular display's stereotypy is not strong, and (3) what behaviors might be only random variability without correlation to intra-display events or social context.

The goals of this paper are to describe the stereotyped aspects of the *A. limifrons* signature display pattern and to show that much of the observed variability is correlated with certain intra-display events.

MATERIALS AND METHODS

Anolis limifrons is a small anole (40 - 50 mm snout-vent length) with a yellow or yellow and white dewlap in males and a much smaller white dewlap in females. The species ranges from southern Mexico to Panama (PETERS & DONOSO-BARROS, 1970), and is relatively well known ecologically (BALLINGER *et al.*, 1970; SEXTON, 1967; SEXTON & HEATWOLE, 1968; SEXTON *et al.*, 1963, 1964, 1971, 1972). Specimens used in our study were collected within a 10 km radius of Gamboa on the South American side of the Panama Canal Zone during the summers of 1972 and 1973. Each individual was toe clipped for permanent identification, with its snout-vent length, weight, and other distinguishing morphological features recorded.

Filming took place during June - August, 1972, in the behavior facilities of A. Stanley RAND, Smithsonian Tropical Research Institute (STRI), Balboa, and from September, 1972 to January, 1974 in the behavior laboratory at Virginia Polytechnic Institute and State University (VPI & SU). At STRI, animals were brought in from the field as the filming schedule required. They were held briefly in several cages exposed to natural temperatures and daylight, and supplied with small crickets and water. When filmed, a subject was brought into the laboratory and placed in a 1.2 m (l) × 0.6 m (w) × 0.7 m (h) glass-fronted plywood enclosure which contained vegetation from the lizards' habitat. The laboratory was kept at approximately 24 C and the lights set on a 12L. - 12D cycle.

In the laboratory at VPI & SU, each of five 1.2 m (l) and 0.6 m (w) × 0.7 m (h) plywood enclosures housed two to three adult males and three to five adult females. The cages contained stumps, branches, and artificial plants. The lizards were fed flies, small crickets, *Tenebrio* larvae year round, and the contents of sweep nets during the summer months. Water was provided in dishes and by spraying the cages daily. Because animals had to be maintained in the lab for most of the year, the fluorescent lights of each cage were set on a 9L - 15D cycle to reduce male interaction and, consequently, better maintain the health of the majority of animals. Though the light-dark cycle was different than at STRI, there was no discernible effect on display variability; displays recorded at VPI & SU and STRI had similar characteristics.

Male displays were filmed under several conditions. The 1.2 m (l) × 0.6 m (w) × 0.6 m (h) photo chambers always contained a resident population of three to five females. At times the subject was the only male in the enclosure. After filming displays which appeared in contexts of little or no agonistic content, another male was added to the cage to elicit more vigorous displaying. At other times displays were filmed from males already dominant over one or two other males in the enclosure. Thus, the recorded displays were filmed within contexts of assertion, courtship, and challenge.

All displays were filmed with a Nizo S80 super 8 camera using Kodachrome II film at 18 fps. Lighting was provided by two Colortran Quartz King 500 floodlights fitted with heat filters. To ensure cool temperatures in the enclosure's interior during filming,

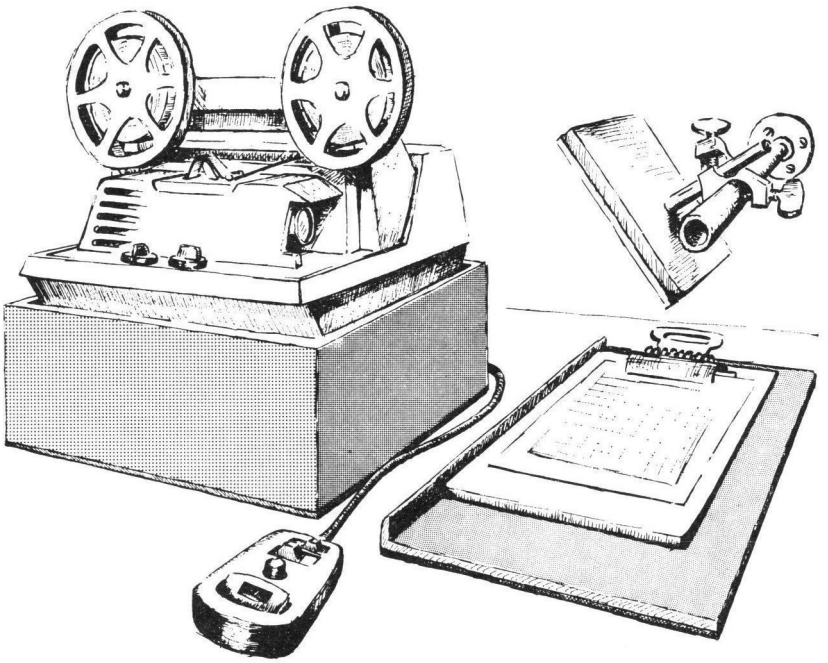

Fig. 1. Equipment setup of frame-by-frame analysis technique.

a fan was situated over the photo chamber to exchange the air within the enclosure with that in the air-conditioned lab.

Filmed displays were analyzed frame-by-frame using a Kodak Ektagraphic MSF-8 projector, support box, mirror, clipboard, and clipboard guide (Fig. 1). Each sequentially viewed frame was projected off the mirror onto the graph paper mounted on the clipboard. Head and dewlap positions were plotted for each frame, and the clipboard was progressively moved along a guide to receive each sequential frame of the movie. The rubber-backed clipboard guide was adjusted before each display so that the projected head movement would be parallel with the y-axis of the graph paper. The movable clipboard guide also allowed compensation during occasional display sequences when the camera moved slightly or the lizard's perch moved (*i.e.*, leaf or twig). Characteristic body movements other than that of the head were noted on each DAP graph along with postural features such as raised nuchal crest and tongue protrusion.

Five distinct display types which incorporate head and dewlap movements or head

movements without dewlapping were recognized in the agonistic behavior repertoire of *A. limifrons* (HOVER & JENSSEN, 1976). One of these, designated the *A* display, is the subject of the present report. It is characterized by the following features: (1) most frequently performed display type in the repertoire, (2) commonly given by a male when concluding a perch shift within his territory, even in the absence of conspecifics, (3) many times used by males as they approach females, and (4) used in male-male interactions, especially during the initial phase of the encounters. Functionally, the *A* display seems analogous to the "A display" of *Phenacosaurus heterodermus* (JENSSEN, 1975), the "signature bob" of *Anolis aeneus* (STAMPS & BARLOW, 1973), the "assertion display" of *A. nebulosus* (JENSSEN, 1970, 1971), and similar to the "assertion-challenge" display pattern used within assertion contexts by most non-anoline iguanids: see reviews by CARPENTER (1967: 87-88) and BUSSJAEGER (1973: 34-36). I will use the term "signature display" to be synonymous with the A display type of *A. limifrons* since this display type appears to function as the basic species recognition and territorial advertisement in the repertoire.

In order to describe its variability, we divided the *A* display into units. Since all uninterrupted *A* displays contained a minimum of seven head bobs, the first seven head movements were singled out for individual analysis. Seven units were established, with each unit consisting of a head bob. A unit was defined as beginning with the initial upward head movement and continuing until the first upward movement of the next bob.

Unit duration was calculated by counting the number of cinema frames which were needed to record a bob; the number of frames was then multiplied by 1/18 to convert to sec. Each of the head bob units comprising a particular display was also expressed as a percentage of the duration of that display's first seven bobs. This latter manipulation was done because an analysis of unit percentages will show how much unit proportionality varies, irrespective of display duration. Unit durations and unit percentages (after arcsine transformation) were then statistically described.

RESULTS AND DISCUSSION

The signature display (*A* display) of *Anolis limifrons* consists of a variable number of head bobs performed in a distinct pattern (Fig. 2). The dewlap begins extension before the first head bob and is held extended throughout the display. Vertical head motion of the display is produced primarily by the neck muscles; though the front legs may be progressively extended during the display, no alternate extension and flexion of the legs (push-ups) occurs.

Head bob dynamics.

The most marked elements of the type *A* display pattern were the relatively high amplitudes and long durations of bobs (Units) 1 and 5 (Fig. 2). There tended to be slight pauses at the ends of Units 1 and 4 and also at the top of the first and fifth head bobs. These features produce an overall impression of a *one large-three small-one large* pattern which is easily distinguished by a human observer. Computation of mean duration for each of the first seven head bobs from a total of 316 filmed displays by 22 males indicated strong stereotypy and little overlap among the seven bob durations (Fig. 3). The total mean duration for these first seven bobs from all *A* displays was 2.73

± SE 0.03 sec, with 95% confidence limits for the mean being 2.68 - 2.78 sec; mean durations of the first seven bobs for individual lizards ranged from 2.08 to 3.20 sec.

The number of head bobs for *A* displays ranged 7 - 27, though all but a single display fell within a span of 7 - 17. The average *A* display for all lizards contained 9.1 ± SE 0.12 head bobs.

Although for each bob duration single classification analyses of variance indicated a significant difference ($P<0.05$) among males (HOVER, 1974; appendix), this interindividual variability in display duration can be expected without necessarily indicating the population reflected a type of behavioral polymorphism. To see if there were a group or groups of lizards whose bob unit durations were distinctly different from the rest of the population

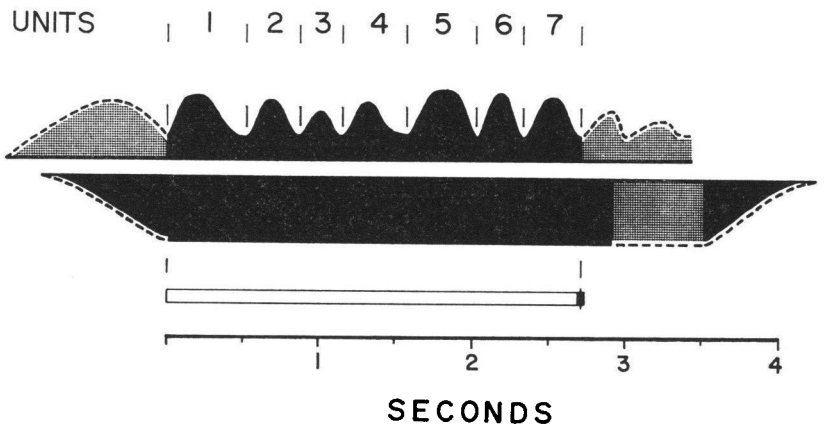

Fig. 2. Generalized DAP graph of *Anolis limifrons* signature display. Stippled areas indicate display components not always present, and dashed lines denote display components not statistically analyzed. Bar below DAP graph gives mean total duration of Units 1-7, its S. E., and 95% confidence limits of mean.

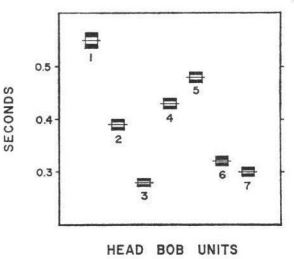

Fig. 3. Mean duration for each of the first seven head bob units in 316 *Anolis limifrons* type *A* displays. Horizontal line indicates unit mean, outer ends of white bars denote standard error of mean, outer ends of black bars provide 95% confidence limits of mean.

sample, a Student-Newman-Keuls (SNK) multiple range test was conducted (SOKAL & ROHLF, 1969). Repeating the process for each of the seven bob units, this test ranked the 22 (number of lizards) mean durations for a bob unit from fastest to slowest and made statistical comparisons between adjacent values of the ranked data. With the exception of bob 6 by male 9, the results were all non-significant (HOVER, 1974; appendix). The range in temporal variation between the lizards' displays was a gradual spread with no evidence toward grouping. In fact this temporal range in bob units for the entire sample was slight as evidenced by narrow 95% confidence limits (Fig. 2).

Single classification of analyses of variance applied to the unit percentages also showed significant differences ($P<0.05$) among males for each of the seven bobs. Here again, the SNK tests found no significant breaks in the ranked data within any of the seven head bob samples (HOVER, 1974; appendix).

Estimates of variance components for each unit indicated that bob duration, expressed either as seconds or as percentage, was more variable within males than among males in *A. limifrons* (Table 1). This is quite different from *A. nebulosus* (JENSSEN, 1971) where 98% of the variation in

TABLE 1

Proportion of variance found within and among males resulting from single classification analyses of variance applied to unit durations and unit percentages of the first seven head bob units of 316 Anolis limifrons *signature displays from 22 males.*

Unit	Source of variation	% Proportionment (unit duration)	% Proportionment (unit percentage)
1	within	61.7	56.3
	among	38.3	43.7
2	within	73.3	84.4
	among	26.7	15.2
3	within	70.8	78.6
	among	29.2	21.4
4	within	59.9	65.8
	among	40.1	34.2
5	within	63.7	64.4
	among	36.3	35.6
6	within	53.7	56.8
	among	46.3	43.2
7	within	63.2	76.7
	among	36.8	23.3
Total duration (Units 1-7)	within	64.3	- - -
	among	35.7	- - -

display duration was in the among lizard component and only 2% of the variability was attributed to the within lizard component. *Anolis limifrons* does not exhibit the intraindividual temporal stereotypy of *A. nebulosus*.

Introductory movement (Roll).

In 153 (48%) of the type *A* displays, the first head bob was preceded by a rolling motion of moderate head amplitude (approximately 1.5 × the amplitude of the first head bob); during this raising and lowering head movement, the dewlap was at least partially extended (Fig. 2). When this movement was absent, the fan was extended with the head held stationary or lowered slightly prior to the first head bob of the display. Without an introductory roll, the dewlap did not reach full extension by the first head bob, but once fully out it remained so for the duration of the display.

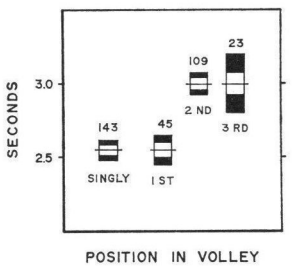

Fig. 4. Mean total duration of the first seven head bobs of the *Anolis limifrons* type *A* display versus when display performed singly or within a display volley. See Fig. 2 for key to statistical notations. Numbers above bars show sample sizes.

Male *A. limifrons* tended to give displays in succession or "volleys" of from two to four displays. It was found that position of a display within a volley correlated with certain variations in display performance. To demonstrate this, type *A* displays were divided into categories depending on whether they were performed singly or were first, second, or third in a display volley. This was done without regard to whether the second or third positioned *A* displays were preceded in the volley by an *A* display or any of several other types in the species' repertoire (*B*, *C*, or *D*).

Comparisons between the above categories indicated several relationships between display variability and position in a display. Displays performed singly or first in a volley had a statistically significant shorter mean total duration for the first seven head bobs than those of displays coming second or third in a volley (Fig. 4). The initial *A* displays of a volley also had significantly ($P<0.01$) more total number of head bobs than *A* displays performed either singly or second and third in a volley (Fig. 5a). Finally, a statistically

significant greater percentage of single and first displays of a volley were preceded by an introductory head movement than second or third displays of a volley (Fig. 6). In summary, *A* displays appearing singly or first in a volley had a fast cadence and usually contained dynamic modifiers (see below) in the form of introductory movements and repetitions of head bobs at the end of the display. These added components indicate a display form of increased elaborateness or intensity. Type *A* displays positioned second

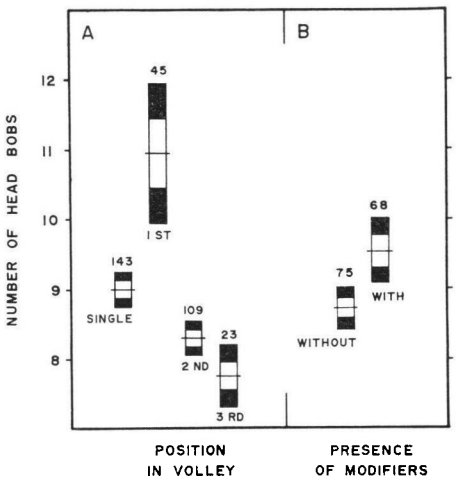

Fig. 5. Mean number of head bobs in the *Anolis limifrons* type *A* display versus: A) when display performed singly or within a display volley, and B) when display performed with or without modifiers present. See Fig. 2 for key to statistical notations. Numbers above bars show sample sizes.

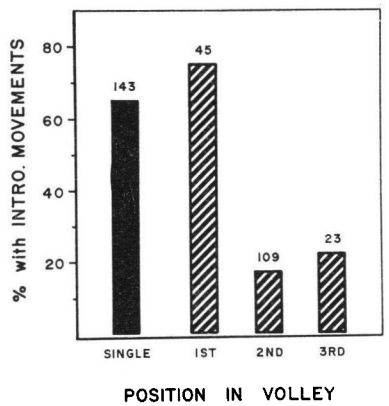

Fig. 6. Percent occurrence of introductory head movements in *Anolis limifrons* type *A* display when display performed singly or within a volley. Numbers over bars show sample sizes.

or third in a volley have significantly fewer dynamic modifiers and are performed with a significantly slower cadence (less elaborate or intense).

Display modifiers.

A display can vary with the appearance of optional display components. In this study it was useful to distinguish between these components and the basic display. To do this, postures or body movements which were not always associated with a particular display type, but could be added to the basic display, were defined as "modifiers." This term was chosen because the auxiliary components physically modify the display and in a grammatical sense may modify the display's information content.

If the modifier is a posture (*e.g.*, lateral compression of body sides, raised nuchal crest, opened mouth), it is considered a "static modifier." If the modifier is a moving body part, it is called a "dynamic modifier." This latter term requires further qualification since some moved body parts (*e.g.*, head and dewlap movements) are used to define display types. A dynamic modifier can be: (1) any occasionally incorporated moving body part besides the head or dewlap which is concurrent or in close temporal proximity to the display (*e.g.*, tail lifts during signature display of *Anolis brevirostris*, JENSSEN, unpubl. data), (2) optional head and/or dewlap movements added just prior to the basic display (*e.g.*, introductory rolling movement of head preceding *A. limifrons A* display), (3) optional head and/or dewlap movements occurring at the end of the basic display (*e.g.*, repetitious bobs following first seven head bobs of *A. limifrons* signature display), or (4) optional repetitions of head and/or dewlap movements which occur just before a transition between qualitatively different segments of a display (*e.g.*, *A. limifrons D* display, HOVER & JENSSEN, 1976: Fig. 5). This last point is an extension of the third condition, and suggests that the *D* display of *A. limifrons* is a compound display. Historically, it may have originated from a welding of three different act systems (a *B* display, a series of 4 legged push-ups, and an *A* display)), with the optional terminal repetitions of each of the three segments being considered dynamic modifiers.

A dynamic modifier should not be applied to any infrequent alterations of head and dewlap movements occurring within the basic display pattern of only a few lizards of a population (*e.g.*, 7% of the sampled *A. nebulosus* occasionally dropped or added a dewlap pulse in their basic signature display, JENSSEN, 1971: 200); this is considered an anomalous condition since it is not performed by the population as a whole. If consistent display variations in the temporal arrangement or qualitative patterning of the basic head and/or dewlap movements appear in an entire population, especially if the

"deviant" displays are performed in uniquely different contexts, then they should be viewed as possibly distinguishing a different display type (*e.g.*, the distinction between *A. limifrons A* and *B* display types, HOVER & JENSSEN, 1976: Fig. 2).

A list of modifiers accompanying the *A* display are as follows:

Static modifiers.

Raised nuchal crest — diminutive in *A. limifrons*, the dorsal fold of skin projecting upward from the neck and anterior back region was only raised during social interaction with a visible subject. The raised crest was a prolonged response and could be up when the animal was not displaying as well as during display. The crest was always associated with prolonged male-male interactions, rarely seen during male-female interactions, and never observed without a conspecific present or recently present.

Lateral compression of body — almost always associated with a lateral presentation toward the object of display. This modifier was associated with prolonged male-male interaction, and never observed without a conspecific present.

Open mouth — the mouth was usually opened wide enough to clearly expose the tongue, and it was held open during part or all of a display. The initiation and duration of mouth opening was quite variable; opening could occur before, but usually during a display. This posture was associated with male-male interactions.

Protruded tongue — the tongue was pushed forward between the lips as a red, pointed protrusion. This could occur as early as during the introductory head movement or during the head bobbing, and could be held for part or all of the display. Its appearance was associated with male-male interactions.

Dynamic modifiers.

Introductory head movement (*Exaggerated roll*) — infrequently the *A* display was preceded by a head raising and lowering of exaggerated amplitude (approximately 3 × the amplitude of the first head bob). Its appearance was associated with male-male interactions, but also accompanied displays directed toward females (12%, 37/430, of female-directed *A* displays).

Introductory head movement (*Roll*) — almost half of the *A* displays began with a moderate raising and lowering of the head (approximately 1.5 × the amplitude of the first head bob) before initiating the display's head bobs. Dewlap extension was usually started during the head raise. It was performed in assertion, courtship, and challenge contexts, and with or without a conspecific present.

Repetitive terminal head bobs — head bobs appearing after the first seven bobs of the *A* display were usually present. The number of these supplementary bobs varied according to social context, position of the display within a volley, and appearance of other modifiers. This modifier appeared with or without the presence of conspecifics.

The appearance of modifiers seems to indicate amplification of an animal's motivational state. Raised nuchal crest, lateral compression of body, open mouth, protruded tongue, and exaggerated roll were almost exclusively used during agonistic encounters. Some of these modifiers appeared more frequently than others, suggesting that there might be a hierarchy of modifier combinations reflecting relative strength of motivational states. Of the 154 filmed *A* displays containing one or more modifiers (exclusive of repetitive terminal bobs and the introductory roll), 96% included a raised nuchal crest; this was usually the first modifier to appear. Accompanying the raised crest in 41% of the modified displays was an open mouth with or without tongue protrusion. Less common (11% of the modified displays) was the Exaggerated Roll; it usually appeared with at least two of the above modifiers.

The Introductory Roll and terminal repetitions of head bobs were frequent modifiers of *A* displays performed during assertion, courtship, and challenge contents. These two modifier types provided the *A* display with a "typical intensity" pattern (for concept see MORRIS 1957). The "typical intensity" pattern of the *A* display was comprised of the basic seven head bob pattern plus a Roll and 1-2 head bobs following the display's seventh bob. Occasionally the *A* displays were performed with no modifiers and a slow cadence (low intensity form) during assertive contexts. At the other extreme the *A* display occasionally contained an Exaggerated Roll, 3-6 Repetitive Terminal Head Bobs, fast cadence, and several static modifiers (high intensity form) during prolonged male-male interaction. However, the "typical intensity" display form was performed most frequently and in a variety of contexts.

When static modifiers were combined with the basic *A* display pattern, the number of Repetitive Terminal head bobs tended to increase. Modified *A* displays had significantly ($P<0.05$) more bobs than unmodified *A* dis-

plays (Fig. 4b). Only displays performed singly were analyzed to avoid a confound with the effects of position upon head bob numbers when displays are given in volleys.

In summary, within the *A* display dewlap extension is stereotyped, as is the *one long-three short-one long* cadence of the first five head bobs. Range of the *A* display's duration for the first seven bobs was fairly narrow. Many aspects of the *A* display, however, showed significant intraindividual variability (*i.e.*, total number of head bobs, appearance of optional introductory head movements, appearance of optional postural components, and speed of display). Much of the *A* display variability within any one individual was found to correlate with intradisplay events (*i.e.*, display position within a volley, appearance of modifiers). There is also evidence that these shifting display features, in turn, are correlated with differing social contexts (HOVER & JENSSEN, 1976). Ultimately, it is hoped the versatility of display form may be proven to convey subtle communicative expression.

SUMMARY

Analysis of 316 filmed type *A* (signature) displays from 22 male *Anolis limifrons* showed that some display aspects were quite stereotyped, while other features demonstrated significant intraindividual variability.

1) Dewlap extension accompanied a basic seven head bob signature display; the head bobbing pattern incorporated a *one long-three short-one long* cadence which was a strongly stereotyped characteristic of the signature display.

2) Range of mean display durations for the sampled lizards' basic display (first seven head bobs) was relatively narrow, being 2.08 sec for the fastest performer and 3.20 sec for the slowest; the population mean and its standard error was 2.73 ± 0.03 sec with a coefficient of variability (standard deviation/mean × 100) of 19.5%.

3) The display duration, however, showed much intraindividual variability; of the partitioned temporal variance, 64% was attributed to the within lizard component and 36% was contributed by the between lizards component.

4) Lizards performed displays in succession, usually in volleys of three displays at a time.

5) Positional effect (whether an *A* display was performed singly or first, second, or third in a volley) was correlated with intraindividual variability of display duration (initial displays were shortest), total number of head bobs in a display (initial displays had more bobs), and appearance of certain optional introductory movements (initial displays more frequently incorporated introductory movements).

6) Increasing number of display head bobs in the *A* display was also correlated with appearance of optional modifiers.

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ZUSAMMENFASSUNG

Analysen von 316 gefilmten Typ A-Imponiergebärden (Kennzeichen imponieren) von 22 männlichen *Anolis limifrons* zeigten manche Imponierungsaspekte als ziemlich stereotypisch, während andere Merkmale bedeutende intraindividuelle Veränderlichkeiten demonstrierten.

1) Sieben fundamentale Kopfnickenimponiergebärden (Kennzeichen) waren von