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Reviewed work(s):
Source: *Copeia*, Vol. 1971, No. 2 (Jun. 1, 1971), pp. 197-209
Published by: American Society of Ichthyologists and Herpetologists (ASIH)
Stable URL: http://www.jstor.org/stable/1442819
Accessed: 12/01/2012 14:44

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1971 No. 2 COPEIA June 1

Display Analysis of *Anolis nebulosus* (Sauria, Iguanidae)

THOMAS A. JENSSEN

A statistical analysis of variation in the assertion display of *Anolis nebulosus* was computed from 599 filmed displays of 59 males. A population-typical assertion display was shared by all examined lizards. Each lizard performed his display-action-pattern with remarkable consistency. The duration of the display's artificially divided units as well as its total sequence, however, showed large variation between individual lizards. No difference in the display pattern appeared when males were compared with females, when lab-held animals were compared with field-filmed individuals, or when lab-held animals were re-examined after a year in captivity. However, display pattern differences did appear when lizards from Nayarit were compared with those from Colima, Mexico. Display analysis can be a useful taxonomic tool for subspecies and species characterization.

INTRODUCTION

BRIEF descriptions of anoline lizard displays have been in the literature for some time. Monks (1881) recorded the head nodding and dewlap pulsing of *Anolis carolinensis* and referred to it as ceremonious courtship. Large aggregations of anoles were observed by Barbour (1926) spreading their dewlaps in the bright sunlight. Noble and Bradley (1933) provided some aspects of the *A. carolinensis* display as it related to courtship and fighting. The sequence of the display of *Anolis sagrei* was outlined by Evans (1938a). Evans (1935, 1936, 1938b) and Greenberg and Noble (1944) also offered more detailed descriptions of the display of *A. carolinensis.*

More objective analysis of lizard displays, however, did not appear in the literature until the advent of the time-motion analysis technique. Carpenter (1961a, b), Carpenter and Grubitz (1961), and Hunsaker (1962) were the first to graph these display-action-patterns (DAP) by using the y-axis of a graph to show amplitude of head movements and the x-axis for the duration of the display. Their work suggested that lizard displays are species-specific. The DAP graph technique and its proposed taxonomic application have been used on a number of iguanid genera (Carpenter, 1962a, 1962b, 1963, 1966, 1967; Clarke, 1965; Ferguson, 1969; Griffith, 1966; Lynn, 1965) as well as *Anolis* (Carpenter, 1965; Garcea and Gorman, 1968; Gorman, 1968; Kästle, 1963; Ruibal, 1967).

From published data, there is growing evidence that iguanid displays are stereotypic and seemingly unique for populations, if not for entire species. However, there is a real need to investigate the possible genetic basis of the saurian display as well as quantifying its stability under varying conditions. And even more fundamental is the need to establish the amount of variation present within the display of a species.

In the present study, the assertion display of *Anolis nebulosus* (Wiegmann) is characterized, and statistical analysis applied to the display's variability. Besides evaluating the effect of aging on the assertive display, this study determines the amount of display variation found within individuals, between individuals, between members of different populations, and between lab-held animals and those in the field. These data are basic to any consideration of a lizard's display being species-specific.

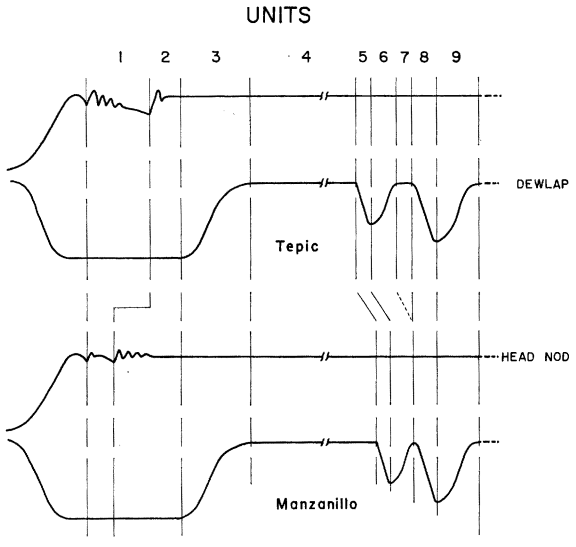


Fig. 1. Diagrammatic assertion displays for two populations of *Anolis nebulosus* showing artificial unit divisions used for display analysis. Vertical axis reflects amplitude of head movement and dewlap extension, and horizontal axis reflects display duration.

Methods and Materials

A statistical analysis of display variation in *A. nebulosus* was computed from 599 displays of 59 adult males. Samples were taken from two populations, one from 35 km east of Tepic, Nayarit, the other from 0.2 km north of Manzanillo, Colima, Mexico. These localities are approximately 250 air km apart.

The displays analyzed were separated into four categories. Displays of 43 males taken from the Nayarit site were filmed in the laboratory. Of these, 13 individuals were refilmed one year later to determine if aging had any effect on a lizard's display. Displays of another 13 lizards on the Nayarit study area were filmed in the field for comparison with displays of lab-held animals. Finally, displays of males collected near Manzanillo, Colima were filmed in the laboratory to check for any interpopulational differences.

The collected males were kept indoors in a room with controlled heat and lighting. During the summer months, however, the temperature frequently exceeded the thermostatic setting, as the lab had no air conditioning. The animals were housed in two 4 × 4 × 3 ft enclosures. To suppress territorial fighting and to retard the establishment of social hierarchies which could possibly affect future behavioral performances, the male lizards were kept in darkened enclosures except for 2–4 hr during their daily feeding period. These laboratory conditions did not seem to alter the display performances, as there were essentially no differences between field and lab-held animals (Fig. 6).

A 6 × 2 × 2 ft observation chamber was used for filming. It was outfitted with a simulated natural microhabitat and stocked with several female *A. nebulosus*. Only one male was ever in the chamber at a time; no male-to-male challenge displays were used. All movies were made during late spring and summer months when males exhibited strong territorial behavior.

After a thorough familiarization with the behavioral repertoire of *A. nebulosus*, the behavior pattern which fit the functional definition of the assertion display (Carpenter, 1962a:137) was chosen for study. This display was the most frequently observed in both lab and field, and the most consistent of the *A. nebulosus* display types. Even when no other lizards were visible, the male often gave the assertion display after reaching a new perch within his territory.

In the field, the activity of *A. nebulosus* was little affected by an observer, even when being observed from only a few yards away. It was then an easy task to film the assertion displays as the males patrolled their territories. In the lab, a male newly introduced

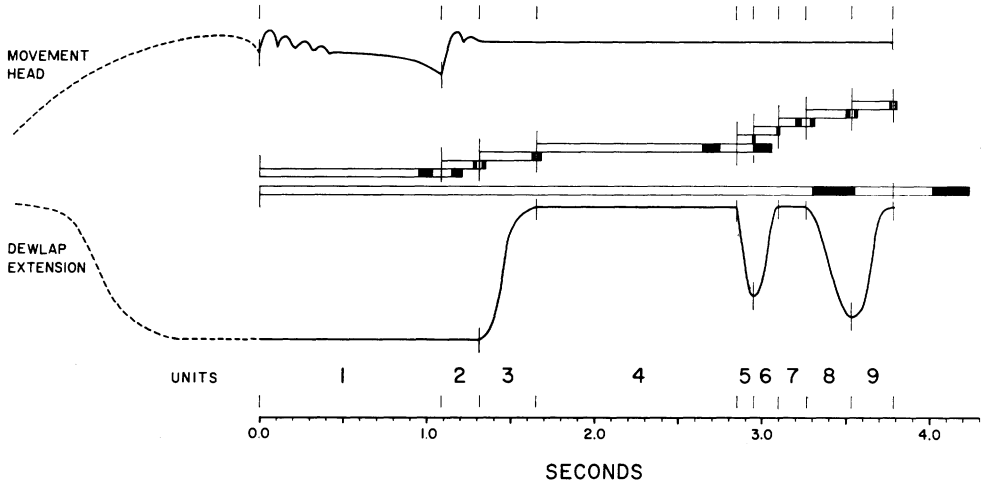


Fig. 2. DAP graph of *Anolis nebulosus* assertion display derived from statistical analysis of 458 displays from 43 lizards collected 35 km east of Tepic, Nayarit, Mexico. Bars indicate duration of each display unit, outer ends of black bars give 95% confidence limits of unit mean, median vertical line between black bars is mean, ends of inner white bars represent standard deviation of mean.

into the filming chamber would begin to display within a day or two. As in the field, the male almost routinely performed an assertion display as he moved from perch to perch in the chamber.

For maximum accuracy, all displays were filmed and then analyzed on a frame-by-frame basis. A Beaulieu (Model 2008S) Super 8 camera was used for all filming. Two quartz iodine flood lights (Colortran Quartz-King Dual 650) provided more than adequate lighting at minimum heat levels during laboratory filming. Frame-by-frame analysis was accomplished on a specially modified Bell and Howell Super 8 projector (Model 482A).

The filming speed for most samples was 18 f.p.s. During some aspects of analysis it was increased to 50 f.p.s. The accuracy of the film speed settings indicated by the camera was checked by filming a stop watch at the two settings. The indicated speed and the actual speed are as follows: 18 f.p.s. (17–18) and 50 f.p.s. (47–49).

During filming, no attempt was made to control the ambient temperature. Temperature may indeed have an effect upon the display speeds of these ectothermic lizards; however, the temporal variability of the displays for each lizard was surprisingly small, as will be shown. The effect of uncontrolled temperatures, therefore, was considered negligible in this study.

For analysis, the display was divided into nine artificial units. These were chosen because of certain clearly recognizable characteristics of the display-action-pattern (DAP) which precisely separated each unit from the others. Each DAP unit was examined separately with a statistical format programmed for the IBM 360/40 computer. The program converted the number of movie frames for each unit to seconds of elapsed time and then calculated the mean, standard error, upper and lower confidence limits (0.95), and maximum-minimum values. The same statistics were computed when each unit was expressed as a percentage of the total display after angular transformation. An analysis of variance was run to compare individual variation with variation in displays between lizards of a sample.

Results and Discussion

This study deals with a number of interrelating factors. However, the laboratory data obtained from the assertion DAP of lizards collected near Tepic, Nayarit will be discussed first and used as a standard. Other factors such as interpopulation differences will be compared to this standard. To facilitate the comparisons, artificial subdivisions of the display pattern were established. Fig. 1 illustrates the criteria delineating the nine units and shows an interpopulation difference in the display pattern of *A. nebulosus*.

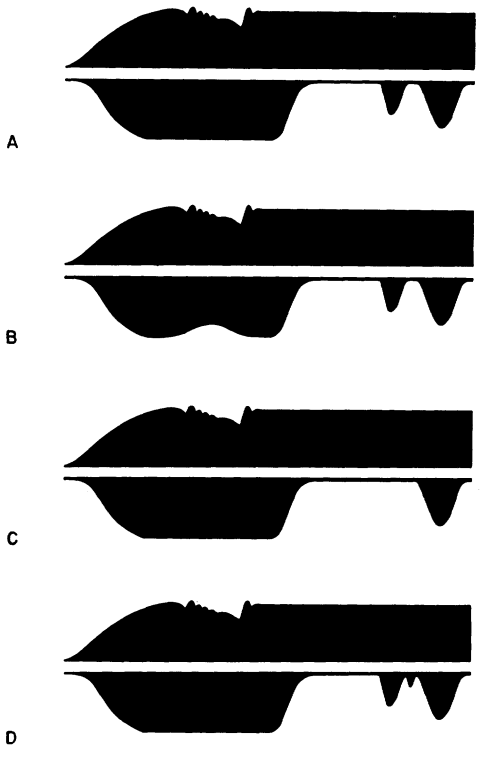


Fig. 3. Four assertion display-action-patterns (DAP) observed in *Anolis nebulosus*. Upper block represents amplitude (vertical axis) and duration (horizontal axis) of head movement and lower block represents dewlap movements. A. Normal assertion DAP; B, C, and D. Deviations from normal assertion DAP.

Units of generalized display.—Initial head raising with concomitant dewlap extension was eliminated from the analysis as this act was temporally variable and greatly dependent on level of excitement and position of the head preceding a display. The first unvarying characteristic of the generalized display is a sharp head nod, perhaps more accurately described as a head jerk; this initiates Unit 1. The head jerk is followed by a series of head bounces of progressively dampening amplitude. A second head jerk follows which marks the end of Unit 1 and begins Unit 2. More head bouncing may or may not follow the second head jerk; if the bounces do occur they are far fewer in number than those following the first head jerk. This concludes all head nodding in the generalized display.

Unit 2 starts with the second head jerk and ends with the initiation of the dewlap retraction. Unit 3 represents the time required for retraction of the dewlap. Unit 4 is a waiting period before the next dewlap extension. Units 5 and 6 are the extension and retraction of the first dewlap pulse. Unit 7 is the waiting period before the extension (Unit 8) and retraction (Unit 9) of the second dewlap pulse. The display analysis ends at this point even though the display is not usually completed until the head is lowered; however, as with the initial head raising, there was considerable variation.

This generalized display-action-pattern for the Tepic population (Fig. 2) was performed with amazing consistency and shared by all observed members of the Tepic population.

Characteristics of atypical and typical displays.—Of 56 males used in the analysis, plus observations on well over 150 other Tepic anoles, only five lizards were seen occasionally performing displays which varied from the generalized pattern (Fig. 3 B–D). One male at times partially retracted and then extended his dewlap during Unit 1. Another male occasionally skipped the first of the two dewlap pulses. The duration of the sequence (total display) of this latter anomalous pattern did not vary from that of the lizard's normal display; instead Unit 4 was lengthened by the amount of time usually occupied by Units 5 and 6 (first dewlap pulse). The last atypical pattern was observed in three males. A weak dewlap pulse sometimes occurred between the two normally occurring pulses. Again, the total display time was identical to that of the animal's normal display. The third dewlap pulse was substituted for Unit 7.

For normally displaying individuals, the temporal intervals of the display units of any one lizard were practically unvarying (Jenssen, 1969:appendix). A lizard performed its assertion display almost identically time after time. Thus, the confidence limits for the duration of the total display were very narrow for each individual (Fig. 4); this was likewise true for each of the nine units. Most individuals, however, were significantly different from other individuals in the time it took to complete a particular unit or the entire display sequence. An analysis of variance for the Tepic population indicated that, of the total variation in display time, approximately 98% was attributed to comparisons between lizards, while only about

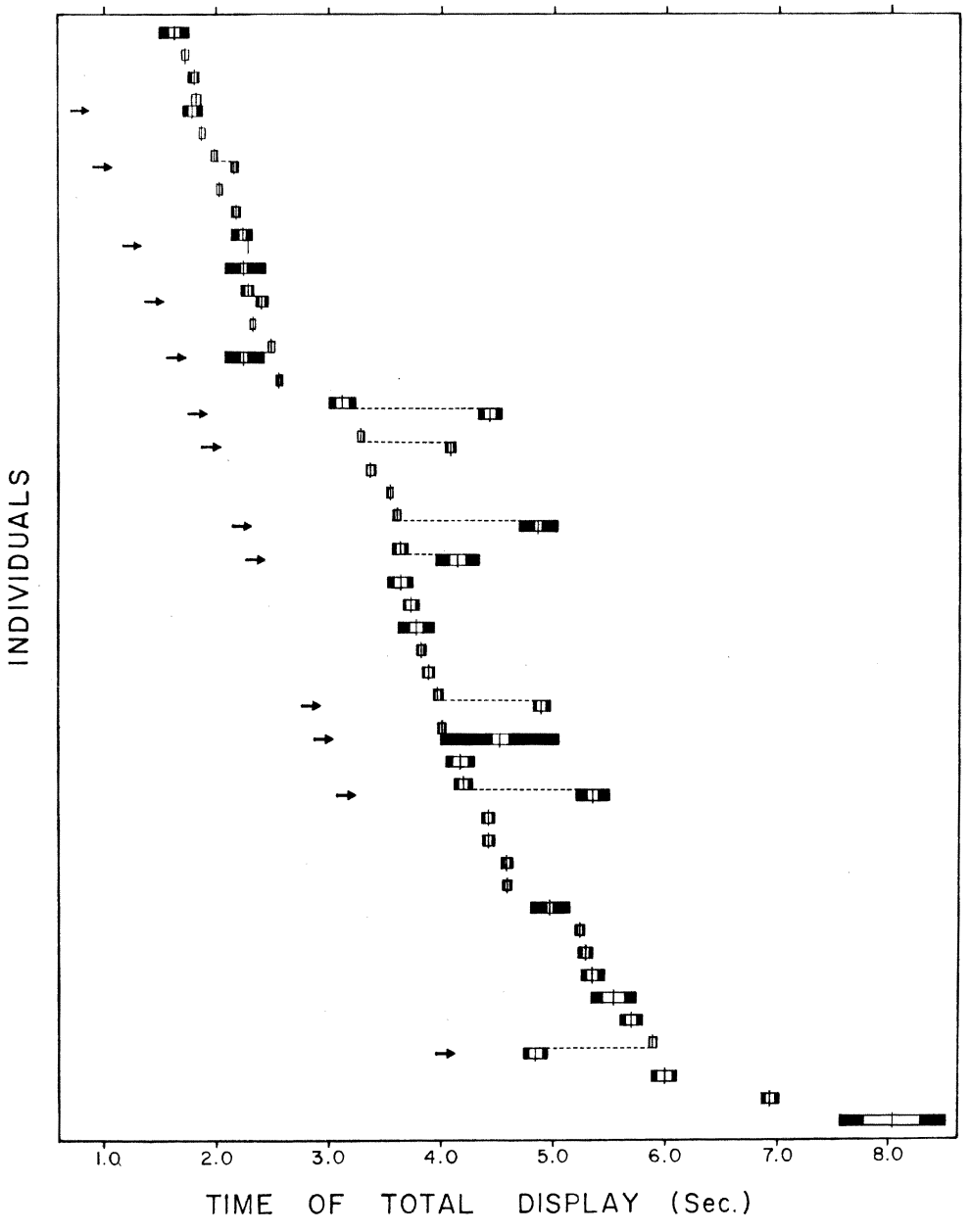


Fig. 4. Duration (in sec) of the total assertion display of 43 *Anolis nebulosus* from Nayarit, Mexico, filmed during summer, 1967; arrows indicate individuals whose displays were again filmed during summer, 1968. Ends of outer black bars give 95% confidence limits of mean, medial vertical line equals mean, ends of inner white bars represent standard error of mean.

2% of the variation occurred when comparing displays of the same individual (Jenssen, 1969:appendix).

Effects of aging on the display.—The displays of 13 males were refilmed one year after their initial filming to see if aging had any effect on the individual display. In the interval between filming sessions, these males increased in size and weight and remained in good health. Ten of the 13 anoles (77%) had longer displays than had been previously recorded. Of these 10, eight possessed sig-

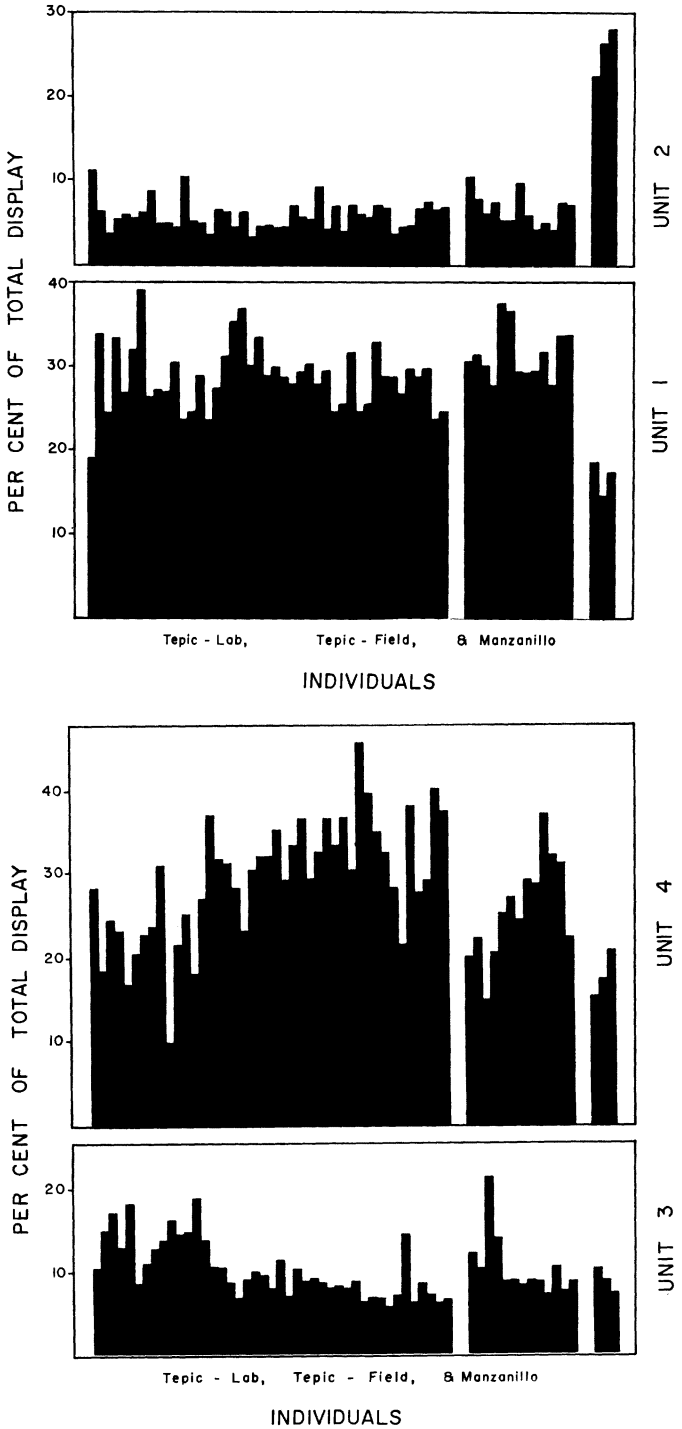
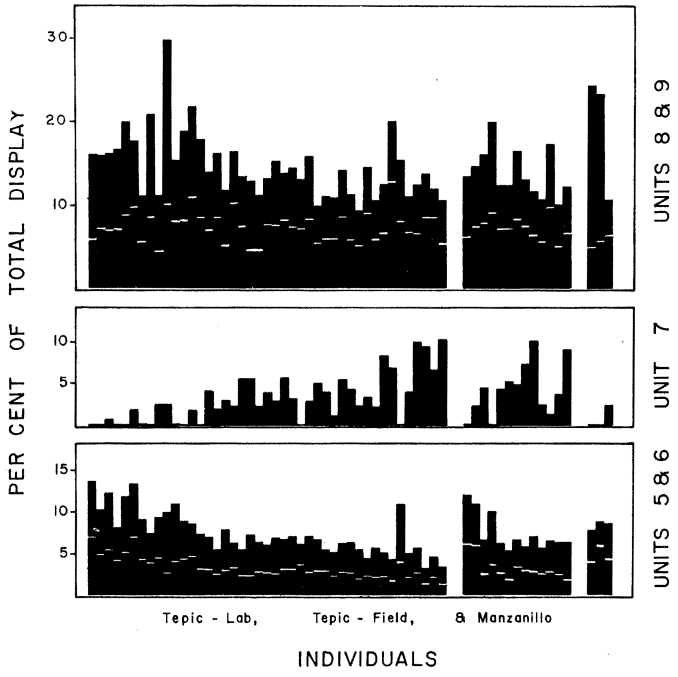


Fig. 5. Units of *Anolis nebulosus* assertion display (as per cent of total display) for 43 lizards from Nayarit, Mexico, which were filmed in lab (Tepic-Lab); 13 lizards collected in Nayarit, and filmed in the field (Tepic-Field); and 3 lizards collected in Colima, Mexico (Manzanillo). Within each block the mean values for each lizard are ordered progressively from the fastest displaying anole on the left to the slowest on the right. (Figure continued on page 203.)



(Figure caption on page 202.)

nificantly longer displays (Fig. 4). There appeared to be a slight lengthening of the display sequence with age.

For most of these "aged" displays the lengthened cadence was reflected proportionally in all units. In the remaining cases, however, only a few units were responsible for the temporal shifts in the total display. Unit 1 deviated significantly in 46% of the refilmed displays and Units 3 and 4 in 48%. These three units were also the longest, with Units 1, 3, and 4 composing approximately 31, 9, and 30%, respectively, of the generalized display.

The trend for displays to lengthen with age suggested that the larger lizards possessed relatively longer displays. To test this idea, the 43 lab-filmed anoles from Tepic were ordered according to their display time, from the fastest to the slowest displaying individuals. This sample was divided into one group of 10 members and three groups of 11 lizards each. The snout-vent length and weight were available for each lizard at the approximate time its displays were filmed. The resulting group averages are as follows: group I (fastest displays)—46.5 mm, 2.57 g; group II—44.8 mm, 2.38 g; group III—44.9 mm, 2.29 g; group IV (slowest displays)—44.6 mm, 2.30 g. There was little difference between the group averages; if anything, the group with the fastest displays had the largest size and weight means.

The tendency for lengthened displays in older lizards appears to be evident only on an individual level. As previously discussed, an individual *A. nebulosus* performed its dis-

TABLE 1. MEAN UNIT VALUES (EXPRESSED AS PERCENT OF THE TOTAL DISPLAY) FOR SAMPLE OF *Anolis nebulosus*—43 lizards from Nayarit, Mexico, filmed in lab (Tepic Lab), 13 lizards from Nayarit, filmed in field (Tepic Field), 56 lizards pooled from Tepic Lab and Tepic Field (Tepic Lab-Field), 3 lizards from Colima, Mexico (Manzanillo), and 10 lizards with fastest displays from Tepic-Lab-Field group (Tepic Fast).

Unit No.	Tepic Lab	Tepic Field	Tepic Lab-Field	Manzanillo	Tepic Fast
1	30.7	31.6	31.0	12.8	29.8
2	5.5	6.4	5.7	27.6	7.3
3	8.8	9.8	9.0	9.2	12.7
4	31.2	26.7	30.2	19.4	22.2
5	2.6	2.9	2.7	5.9	5.2
6	3.6	4.0	3.7	4.0	5.8
7	4.1	4.7	4.2	1.0	0.6
8	7.1	7.3	7.1	5.9	7.4
9	6.4	6.6	6.4	15.2	9.0

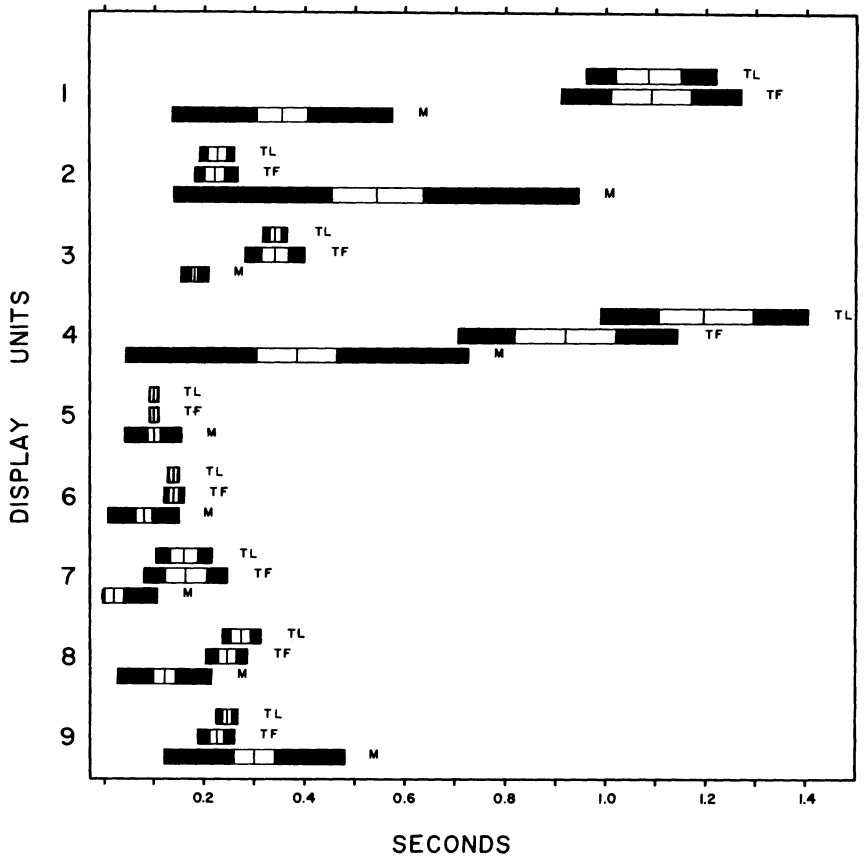


Fig. 6. Duration of units of the *Anolis nebulosus* assertion display from 43 lizards collected in Nayarit, Mexico and filmed in lab (TL), 13 lizards from Nayarit filmed in field (TF), and 3 lizards from Colima, Mexico (M). Ends of outer black bars give 95% confidence limits of mean, median vertical line equals mean, ends of inner white bars represent standard error of mean.

play with almost no variation in duration. Very little change in cadence would thus effect a significant difference from the lizard's previous displays; such was the case in eight of the anoles refilmed after a 12 month interval. These slight, but statistically significant, individual differences were masked when the population was viewed as a whole because of the large variation between lizards.

Relationship of cadence to the display.— Display times varied greatly in the sampled *A. nebulosus.* Some lizards completed a display sequence in less than two seconds, while others required almost eight seconds to finish (Fig. 4). The question arose as to whether each unit remains proportionally similar no matter what the total display time may be. To derive an answer, all displays were made comparable by expressing the time interval of each unit as a percentage of its display's total duration. To make this calculation explicit, the following is offered: taking a single display, all of its nine units were converted to a percentage of that display's total duration; together the units equal 100%. This was done for all displays from a single lizard. Then the percentage mean was calculated for each unit from all displays of that lizard. This last procedure was duplicated for the 59 anoles in the sample (Fig. 5).

Units 1 and 2 in the Tepic sample revealed no consistent alterations in proportional importance with changes in total display duration (Fig. 5). Unit 3, the interval required to retract the dewlap, usually decreased in its percentage as the display lengthened. To some extent this was because

many lizards retract their throat fans at about the same rate. Therefore, this unit's per cent would decrease as the total time of the display increased.

Unit 4, a waiting period before the dewlap pulses, was primarily responsible for increasing the duration of the Tepic display (Fig. 5). Lizards with long displays show a large disproportionate increase in this unit. The per cent importance of Units 5 and 6 (the first dewlap pulse) reduced progressively as the display time lengthened. Although this percentage reduction was not as marked as in Unit 3, it reflected the consistent rate of dewlap extension and retraction regardless of display duration.

A relationship exists between the proportion of Unit 7 and the speed of the display. Those lizards possessing fast displays usually lacked Unit 7; as the display increased in length, however, this unit appeared and correspondingly lengthened in duration (Fig. 5). The percentages for the dewlap extension and retraction of the last pulse (Units 8 and 9), showed a very weak tendency to decrease as the display increased in time.

Four generalizations can be made from this analysis. 1) The initial two units increase proportionally as the total display lengthens, thereby maintaining their per cent importance. 2) Those units defined by dewlap movement (3, 5, 6, 8, and 9) tend to have their percentages reduced as the display lengthens. This is due partially to a relatively constant rate of extension and retraction of the throat fan irrespective of display duration. 3) Unit 7 is absent in the displays of most lizards which perform quickly. The per cent importance of this pause between the dewlap pulses appears and increases as the display lengthens. 4) As a display increases in duration, the majority of the added time is taken up by Unit 4.

Effect of environment on the display.— Lizards from the Tepic population were filmed in the field to determine if any display aberration occurs in confined animals. Fifty-six field-filmed displays were recorded from 13 male anoles. These were compared with 458 lab-filmed displays from 43 other anoles.

Statistical comparisons of the field-filmed with the lab-filmed groups revealed little difference (Fig. 6). Only Unit 4 varied, and this difference was not significant. No significant differences were evident when the units were expressed as a percentage of the total displays and compared on an individual basis. Both unit percentages and unit times for field displays fell within the range of corresponding lab derived values. Few differences were apparent when the averages for the units of each sample were converted to percentages and compared (Fig. 5, Table 1).

Comparison of inter-population displays.— There was a major difference between the displays of *A. nebulosus* collected near Tepic, Nayarit and those from Manzanillo, Colima. Units 1 and 2 were reversed when comparing the two populations (Figs. 1, 5, 6, and Table 1). Unlike the Tepic lizards, Manzanillo *A. nebulosus* produced more head bouncing after the second head nod than after the first; no exceptions to this were observed.

There may also be minor variations between the displays of the two populations. However, as the Manzanillo population was represented by only three lizards, generalizations for more subtle display characteristics must be cautiously applied.

The three Manzanillo males had displays averaging 2.08 sec duration as compared with a 3.76 sec mean for the Tepic anoles. However, a few Tepic individuals had displays as fast as the Manzanillo lizards. Most unit differences between the two populations appear related to the speed of the display, for as the duration of the displays decreased, the units became crowded with certain unit percentages decreasing disproportionally (Jenssen, 1969:appendix). This relationship between display speed and changes in the unit percentages was tested by comparing 10 of the fastest displaying anoles from Tepic (mean display duration 1.90 sec) with the Manzanillo lizards (Table 1). The rapidity of the display appears responsible for the Tepic–Manzanillo differences in Units 4, 5, 6, 7, and possibly 8 and 9. As mentioned previously for the Tepic sample, as a display increased in duration, the unit percentages tended to increase for Units 4 and 7 and decrease for those units involved in the dewlap pulses (3, 5, 6, 8, and 9). These trends seem to explain most of the Tepic–Manzanillo display differences.

The important distinction between the displays from the two populations is the transposition of Units 1 and 2. This constitutes a basic alteration in the sequence of motor patterns and, therefore, produces a

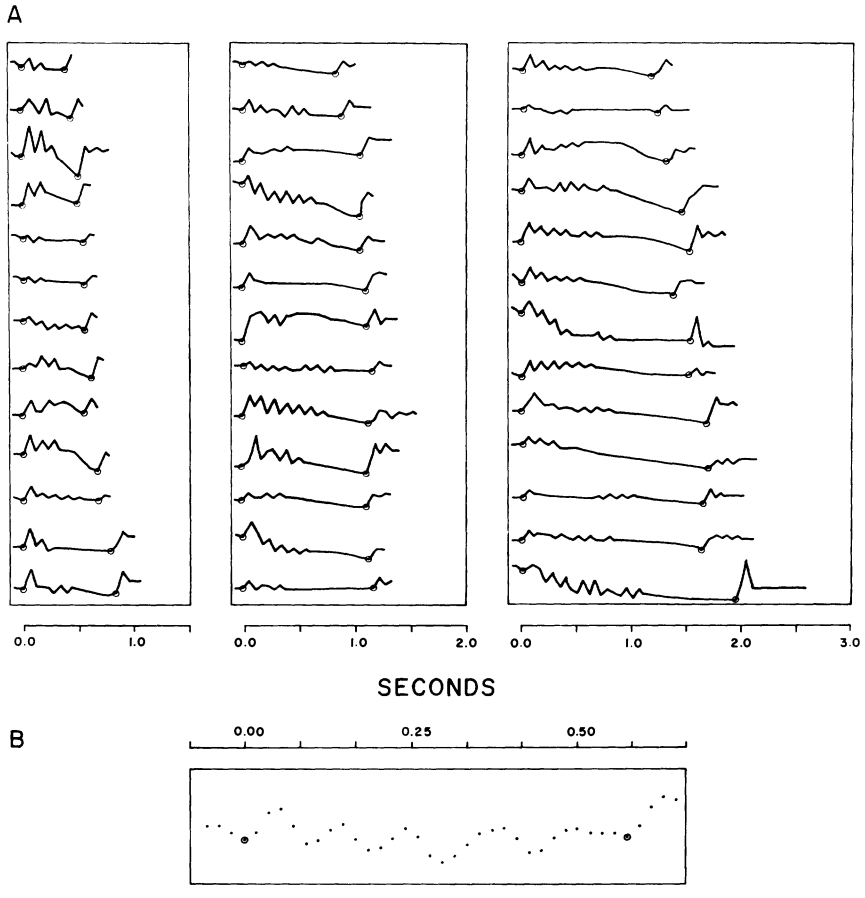


Fig. 7. DAP graphs for Unit 1 and part of Unit 2 of *Anolis nebulosus* assertion display from individual lizards collected near Tepic, Nayarit, Mexico. A. traced from displays filmed at 18 f.p.s. B. traced from display filmed at 50 f.p.s. Circles denote beginning of Units 1 and 2.

display pattern unlike the Tepic display. As all observed Tepic anoles performed the same generalized display pattern, it is quite probable that the three males from Manzanillo accurately reflect a generalized DAP typical for their own population.

The differences between the *A. nebulosus* assertion displays of the Tepic and Manzanillo populations may actually reflect inherent genetic differentiation. The Manzanillo collected males had a broad white band on the anterior margin of their dewlaps; this pattern was not shared by the Tepic specimens. These data tend to support Hobart Smith's belief that *A. nebulosus* may be a polytypic complex rather than a single variable species (pers. comm.). The observed combination of behavioral and morphological differences between closely related forms suggests the potential of saurian display analysis as an additional criterion for taxonomic determinations.

Individual variation.—Besides temporal variation, other aspects of the Tepic display varied between individuals. The head nodding sequence of Unit 1 and part of Unit 2 was a good example of individual variation. Comparisons between individuals showed a wide range in the number of head bounces following head jerks, although all Tepic lizards bounced more after the first head jerk than the second (Fig. 7). Displays whose first two units were of long duration contained the greatest number of head bounces. Averages for 43 lizards showed 4.1 bounces after the first head jerk and 1.4 bounces after the second.

There was also considerable variation in

head deflection during the head nodding; this movement ranged from shallow to very exaggerated nods. It appeared that each lizard possessed its own characteristic amplitude. Yet, precise quantification of head amplitude was impractical since camera angle, distance from camera to subject, and subject size were never consistent.

Tracings made of each lizard's head nods (Fig. 7A) were taken from sequences shot at 18 f.p.s. This filming speed caused the head bounces to graph as spikes. When filming at 50 f.p.s., however, the bounces of even the most rapidly displaying lizard appeared as rounded waves (Fig. 7B).

Amplitude of the dewlap pulses was also a source of individual variation. From a sample of 43 lizards, 72.1% performed displays in which the second pulse had greater amplitude than the first. A few individuals (16.3%) gave pulses of approximately equal extension. Least common (11.6%) were anoles with displays having the first pulse of greater amplitude. For the sample, the relative extension of the first and second pulses averaged 67% (S.D. ± 10.4%) and 81% (S.D. ± 8.0%), respectively, as compared with the initial throat fan expansion during head nodding (100%).

Male and female displays.—In comparison with males, female *A. nebulosus* have a diminutive throat fan. The pinkish fan also differs in color from the male's. Females use these smaller dewlaps in the same ways as do the males (Jenssen, 1970). The filmed assertion displays from seven females of the Tepic population showed no deviations from the generalized DAP determined for the males.

Social function of assertion display.—The assertive display was selected for analysis after three months observing and characterizing the behavioral repertoire of *A. nebulosus*. This display appeared to function as a territorial declarative and species recognition signal (Jenssen, 1970). There is also evidence that the male's assertive display can attract females into his territory (Jenssen, 1971). This suggests the male assertion display may be used by females in mate selection; it can also act as an isolating mechanism. Such a behavioral pattern would need to be consistent and unique for at least an interbreeding population; this is true of the *A. nebulosus* assertion display.

Taxonomic and systematic value of assertion display and other social behavior.—The assertion display seems well suited for distinguishing between species and subspecies, and, therefore, is useful taxonomically. However, the display's application to systematics may be limited. If the assertion display is used for species recognition and mate selection, it would be strongly selected for its distinctiveness from the assertion displays of other lizard species, particularly congeners. Thus, there may be sufficient divergence between closely related species to limit the systematic value of such species distinct characteristics beyond the specific or generic level (Sibley, 1957:187).

The *A. nebulosus* challenge display is a discrete behavioral entity and is similar in form to the assertive display (Jenssen, 1970). The challenge display tends to share the assertive display's stereotyped quality. However, because of the intensity of male—male encounters, the challenge display can become exaggerated. For this reason it is not as stable as the assertion display. Though it also has taxonomic value, the challenge display would not seem as sensitive a taxonomic criterion.

Theoretically, the behavior which may hold the most promise for phylogenetic comparison is the challenge encounter. This includes the challenge display and all associated aggressive behavior, including posturing. In avian studies where much more behavioral work has been done, the similarities in aggressive behavior of related species is well documented (Marler and Hamilton, 1966:375). Miller (1968:62) did not believe it is merely fortuitous that sympatric species share many behavior patterns. The retention of behavior patterns which are common to competing species permits interspecific communication and is an effective mechanism in the process of competitive interference. However, many interspecific comparisons will be needed before the challenge encounter can be adequately evaluated as a phylogenetic criterion.

Conclusions

An objective of this analysis was to determine how specific the assertion display pattern is for a population of lizards. Comparisons between animals showed considerable differences in the lengths of the display. Each individual, though, performed its own display with amazing temporal consistency.

But more importantly, the population shared without exception a common display pattern. The various motor acts which compose this display sequence were present in the displays of all members of the population and were rigidly ordered. A very few lizards occasionally gave an altered version of the generalized pattern, but they were also seen displaying normally. The Tepic population of *A. nebulosus* possessed a stereotypic assertion display (Fig. 2). Such a stable characteristic should be of taxonomic value.

The study also revealed an interpopulational difference in the assertion display. In widely distributed lizards such as *A. nebulosus,* population to population differences in the display may be significant, as appears true for *Uta stansburiana* (Ferguson, 1969; McKinney, 1971). Whether the interpopulational variation in the *A. nebulosus* assertive display reflects a difference in taxa has not yet been determined.

ACKNOWLEDGMENTS

Dr. Charles C. Carpenter is gratefully acknowledged for his encouragement and advice during this study. The presented data represent a portion of the research conducted as a requirement for the doctorate in zoology at the University of Oklahoma. Financial support was generously provided by a N.I.H. predoctoral grant (5-F1-GM-33,435).

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Patterns of Heat Distribution Within the Bodies of Some Australian Pythons

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Data on carpet pythons (*Morelia spilotes*) in confinement and from the field suggest that their preferred temperature is *ca.* 30° C and that the upper limit of temperature range voluntarily accepted is just above 34° C. When a snake is uniformly heated, the head temperature rises faster than that of the body until it reaches 30° C (near preferred temperature) after which it remains nearly constant, though body temperature continues to rise. The circulatory system greatly affects heat distribution patterns within the animal. Changes in heart rate and corresponding abrupt thermal changes in various parts of the body occur during local heating of the head and anterior neck. This suggests that head-body temperature differences are influenced by release of warmed blood from the head and by more rapid flow of cool blood from the posterior extremities when head temperature approaches the upper limit of the preferred range. Another Australian python, *Liasis amethistinus*, seems to have similar temperature characteristics.

INTRODUCTION

SUGGESTIONS that reptiles can influence the distribution of heat within their bodies have been presented in the literature. Postulated mechanisms have been: 1) changes in flow rate in peripheral blood vessels in response to local body temperature variation (Cowles, 1958; Morgareidge and White, 1969; Weathers, 1970), 2) a shunt in the drainage of cephalic venous sinuses which permits voluntary inclusion or exclusion of an internal jugular-internal carotid counter-current system (Heath, 1966), and 3) increased cardiac output to the body associated with partial bypassing of the pulmonary circuit, made possible by paired systemic arches and their relation to the incomplete ventricular septum (Tucker, 1966, 1967; Baker and White, 1970). The latter mechanism, however, may not be applicable to all reptiles, as Johansen (1959) found low blood resistances in the pulmonary circuit of two species of snakes. Bartholomew and Tucker (1963) concluded that as much as three-fourths of the difference between heating rate and cooling rate of the bearded dragon (*Amphibolurus barbatus*) resulted from circulatory effects (the remaining one-fourth was derived from metabolic heat production).

No comparable data have been published for snakes, although Campbell (1969) referred to unpublished data on head-body temperature differences, and Benedict (1932) noted that rectal and mouth temperatures of confined regal pythons (*Python reticulatus*) often differed by as much as 0.7° C. Strelnikov (1944) stated that temperature differentials as great as 7° C occurred within the bodies of lizards and snakes. Also, snakes can thermoregulate by selecting appropriate environmental temperatures, basking, making postural adjustments (*e.g.* coiling, flattening the body), aggregating (Carpenter, 1956; Fitch, 1956; Cogger and Holmes, 1960; Stewart, 1965; Regal, 1966; Myres and Eells, 1968;