# THE ONTOGENY OF DISPLAY BEHAVIOR IN SCELOPORUS UNDULATUS HYACINTHINUS (SAURIA: IGUANIDAE)

by

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# Introduction

The head-bobbing displays of agamid and iguanid lizards have long been assumed to be an instinctive and species-specific class of behaviors (Carpenter, 1967: 102). Yet almost nothing is known about the ontogeny of reptilian display patterns. There are only anecdotal observations on hatchling displays (Carpenter, 1960; Cooper, 1971; Jenssen, 1970; Yoshida, 1966), a longitudinal study of *Anolis nebulosus* adult display patterns (Jenssen, 1971), and a cross-sectional analysis of displays in different age classes of *Anolis aeneus* (Stamps, 1978). To date, however, there are no longitudinal data on the early development of display behavior for any saurian species.

The present investigation is a laboratory study of the development of display behavior by *Sceloporus undulatus hyacinthinus* that provides a quantitative analysis from hatching to adulthood for individual lizards from several different clutches. The objectives of this study were: (1) to determine when the hatchlings first performed the adult display patterns; (2) to catalog and quantify any changes that appeared in the pattern of the displays over time; and (3) to compare features of the displays both within and between clutches as a means to evaluate the genetic influence on display behavior.

# Materials and Methods

## Subject

The fence lizard, Sceloporus undulatus, has a wide distribution in the United States, where it is represented by six geographic forms (Tinkle and Ballinger, 1972). I studied S. u. hyacinthinus, the only sceloporine north of Georgia and east of Texas (Conant, 1975). This lizard is relatively small (maximum SVL = 83 mm), gray or brown in color, largely arboreal, and is an inhabitant of woodland edges.

Rothblum and Jenssen (1978) studied the display behavior of adult male S. u. hyacinthinus, and their study served as a base of comparison for my research. They described two similar, but distinct, display patterns, designated Type A and Type B (Figs. 1 and 2). These two display types had core patterns (i. e., the part of the display that is always performed) of four plateaued bobs separated by three interbob pauses. In most displays, the core pattern was followed by a varying number of identical terminal bobs. For purposes of analysis, every bob and every interbob pause was isolated and each designated as a unit. The units of a display were consecutively numbered, such that the bobs constituted odd numbered units and the interbob pauses were even numbered units (Fig. 1).

The major distinction between the A and B patterns was that the Type A displays had longer bob durations and shorter interbob pause durations than the corresponding units of the Type B displays; almost all of the corresponding A to B unit comparisons were found to be statistically significant. This difference was exemplified by the ratio of the durations of Unit 2 / Unit 3; in general, this ratio was less than 1.0 for A Displays and greater than 1.0 for B Displays (Fig. 3). Another difference between the display types was in the relative amplitudes of bob 3 / bob 4; their amplitude ratio was greater than 1.0 for all A Displays and less than 1.0 for most B Displays.

Rothblum and Jenssen (1978) found the Type A displays to be very stereotyped both within and among adult lizards. In contrast, more than half the observed males consistently performed individually unique variations of the Type B pattern by either deleting a bob, exaggerating the amplitude ratio between adjacent bobs, or performing dips before the terminal bobs (Fig. 2). Therefore, no single Type B pattern was characteristic of the population. This apparent combination of a stereotyped behavior at the population level (Type A Display) and of patterns that are distinct at the individual level (Type B Display) provided a promising opportunity to examine ontogeny and heritability in a vertebrate communication system.

## Source of Lizards and Laboratory Maintenance

Gravid female lizards were collected at an abandoned coal mine 10 km west of Blacksburg, Montgomery County, Virginia in June 1978, 1979, and 1980; this was the same collection site used by Rothblum and Jenssen (1978). Eggs laid by these females were incubated at about 30° C in either vermiculite and water (50:50 by weight) or sand and water (15:1 by weight). Aside from one clutch in which the eggs failed to develop, hatching success was 98%. No more than 5 individuals per clutch were studied in 1978 and 1979, whereas all 10 individuals from one clutch were studied in 1980. Eight clutches and 36 individuals were observed during the three years of my study.

Hatchlings were toe-clipped for individual identification, and sexed by the size of the post-anal scales; 9 lizards from two 1979 clutches were not sexed. Hatchlings were maintained in groups of 1-10 in glass aquaria ranging in size from 38-151 l. Each cage was provided with stumps, sticks, soil, and bark litter. A natural (seasonal) photoperiod was supplemented with both fluorescent Vita-lites and incandescent lights with metal reflectors. Temperatures in the cages ranged up to 38° C during the light cycle and down to 18° C during the dark cycle. Water and food (field sweepings, nymphal crickets, and mealworms) were supplied daily. A powdered vitamin and mineral supplement was dusted onto the food several times a week.

### Analysis of Displays

Video tape recordings of displays were made using a JVC video camera with a Fujinon 12.5-100 mm zoom lens, and a Sanyo VTR 1200 video tape recorder with 60 frames/s resolution and frame-by-frame playback capability. An Odetics G-77 Video-Date Time Generator provided a superimposed image of date and elapsed time in 0.01 s increments during recording sessions.

For most hatchlings (75%), taping was begun on the day of hatching, and data collection was concentrated on the earliest ages of all subjects. An effort was made to tape each lizard daily during the first week post-hatching, weekly during the following month, and approximately monthly thereafter; video tapes of 1979 lizards, however, were made during the first month only. Time constraints, deaths of some lizards, and the failure of some lizards to display for long periods of time produced a variable video tape record for some 1978 and 1980 lizards (Appendix I).

Before each recording session, lizards were given a coded mark with acrylic paint to facilitate identification during playback. To increase the frequency of displays during a taping session, several different techniques were used: 1) moving the lizards to a cage other than their home cage; 2) presenting the lizards with conspecifics other than their usual cagemates; 3) providing food; 4) moving the lizards to a cage recently occupied by an adult conspecific; and 5) introducing a novel object. One or more of the first three techniques was used in every session; the latter two were used only rarely.

Recorded displays were played back frame-by-frame into a Sony 19-inch TV monitor. Changes in the lizard's head amplitude were measured along a transparent grid overlaid on the TV screen; every amplitude change was recorded to the nearest mm, along with the time of its occurrence (from the date-time generator) to the nearest 0.01 s. The year, month, day, hour, and minute of the display were also recorded. The resulting primary data were subsequently used to draw a Display-Action-Pattern (DAP) graph for each display, as described by Carpenter and Grubitz (1961) and Jenssen (1978), with time on the horizontal axis and head amplitude on the vertical axis.

Each display was divided into units as described by Rothblum and Jenssen (1978). For bob duration, Rothblum and Jenssen (1978) measured only the plateaued portion of each bob, excluding the ascending and descending head movements (Figs. 1 and 2); I included these movements in the bob durations. Twelve units--the first six bobs and the first six interbob pauses--were included in this study. Lizards frequently performed displays with more than two terminal bobs, but the additional bobs were not measured because the terminal bobs were essentially identical to one another (Rothblum and Jenssen, 1978). However, the number of terminal bobs was counted as part of the total number of bobs per display.

Most of the hatchling displays could readily be designated as either Type A or Type B by visual inspection. The displays of some individuals, however, appeared to have characteristics intermediate between those of the A and B Displays. In these cases, the summed duration of the first five bobs was subtracted from the summed duration of the first five interbob pauses for each of the lizard's displays. A plot of these remainders showed a clearly bimodal distribution. Because A Displays were described as having longer bob and shorter interbob pause durations than B Displays (Rothblum and Jenssen, 1978), the larger remainders were assumed to represent B Displays and the smaller remainders were assumed to represent A Displays. The very few (less than 1%) displays that remained ambiguous were excluded from the analysis. My final data set contained 554 A and 389 B Displays (Appendix I).

As a check against my Type A-Type B designations, a Discriminant Function Analysis (Jenrich and Sampson, 1979) was performed on all displays. This program used several discriminating variables (durations of Units 1, 2, 3, 4, 7, 8, and 9; Ratio and Keyratio (Table 1)) to assign all displays to one of two groups. The Discriminant Function Analysis agreed with my designations of displays as Type A or Type B for 99.4% of A Displays and 97.1% of B Displays (Fig. 4). The three most important variables for making the discrimination were the durations of Units 3, 4, and 9.

### Data Analysis

Twenty-five variables for each display, including the durations of Units 1 - 12, were used in my data analysis (Table 1). Unit durations were determined to the nearest 0.01 s by subtraction of the beginning time from the ending time of each unit. To facilitate evaluation of ontogenic changes, each display was labeled according to the age in days of the displayer. This linear time scale was also used to define two other time categories, Weekgroup and Agegroup (Table 2). The Weekgroup and Agegroup categories are non-linear, with their initial subdivisions covering shorter time periods than subsequent subdivisions. This uneven scaling produced a more balanced distribution of sample sizes among the subdivisions, and yielded a finer resolution during early time periods when the rate of ontogenic change was suspected to be greatest.

The distribution of unit durations was normal in almost all cases (Kolmogorov-Smirnov goodness of fit tests);

therefore, parametric tests from the Statistical Analysis System (Barr, et al., 1979) were used for all computer analyses. Because sample sizes were unbalanced, the General Linear Model procedures were used rather than Analysis of Variance. The Variance Components Procedure (Barr, et. al., 1979) was used to estimate the percentages of total variance attributable to different factors.

# Results

## General Observations on Initial Displays

Hatchlings began to display almost from the moment they became active after hatching. Of the 26 hatchlings that were first taped on the day of hatching, 11 (42%) performed at least one display on the hatching day (day 0), 16 (62%) by day 1, and 24 (92%) by day 2. Displays of the two remaining lizards were not observed for 3 or 4 months. These hatchlings were generally inactive and often hid in crevices or in the cage litter during taping sessions.

Although the first display performed was usually a Type A display (80% of the cases), 75% of the hatchlings performed both Type A and Type B displays within three days of hatching. Two lizards, however, did not perform any B Displays in the seven months during which they were taped. Excluding these two, an average of 2.38 (range 0 - 9) A Displays were recorded before the first B Display was recorded. Three hatchlings performed a "jiggle" (Rothblum and Jenssen, 1978) on the day of hatching, even though this behavior was rare among older hatchlings.

The very earliest displays sometimes had very low amplitudes and often consisted of only two or three bobs. Among the 168 displays recorded within the first three days, 11% had two bobs, 37% had three bobs, 30% had four bobs (the core pattern), and 22% included the core pattern plus one or more terminal bobs. The hatchlings performed an average of only 1.33 (range 0 - 6) abbreviated displays prior to performing a complete core pattern; however, some two- and three-bob displays were performed after the complete core pattern first appeared.

In 49% of the displays performed within Weekgroup 0.5 (Table 2), the third and fourth bobs were given as a single bob or as a single bob that was stepped (Fig. 5 and Table 3). Sixty-eight percent of the displays in Weekgroup 0.5 had bobs that were "rounded" rather than "squared"; that is, the lizard's head ascended and descended slowly rather than abruptly (Table 3). Both of these characteristics were less frequent in later Weekgroups (Table 3).

### Ontogenic Changes from Hatching to Maturity

Changes in Display Frequency. The frequency of displaying did not vary significantly between Agegroups of a sex or between sexes of an Agegroup ($P > 0.05$, Mann-Whitney U Test), although there was a tendency for both males and females to display more frequently with age (Table 4). Variability among individuals was high, as indicated by the large standard errors for the mean frequency of displaying (Table 4). Some individuals averaged less than one display per hour, while one male performed 34 displays per hour in Agegroup 3.

Changes in Total Bobs. For both A and B Displays, there was a significant increase from Agegroup 1 to Agegroup 2 in the total number of bobs per display ($P < 0.001$, Mann-Whitney U Tests; Table 5). There was also a slight increase from Agegroup 2 to Agegroup 3. However, even in Agegroup 1, almost all displays included the core pattern (i. e., the first four bobs).

Changes in Ratio of A:B Displays Performed. Both male and female lizards tended to perform more A than B Displays (Table 6). With displays pooled for males and for females in each Agegroup, the A:B ratio for males remained relatively constant across the three agegroups, dropping slightly from 1.3 to 1.2. Females tended to have higher A:B display ratios than males, and those in Agegroup 3 had the highest ratio, which was significantly different from that of males in all three Agegroups as well as from females in Agegroup 2 (Table 6).

A:B ratios for individual lizards, however, varied considerably. Ratios for individual males ranged from 0.53 (9A:17B) to to 4.00 (28A:7B), with a mean ratio among males of 1.51 ± SD 0.99. For females, individual ratios ranged from 0.83 (25A:30B) to 9.00 (18A:2B), with a mean among females of 2.96 ± SD 2.49. The mean ratios among individuals were higher than the pooled ratio values because lizards with ratios closer to 1:1 performed more displays than lizards with higher ratios; consequently, the former lizards were more heavily represented in the combined data.

Changes in Display Pattern. The overall pattern of most displays was the same as that found by Rothblum and Jenssen (1978) for adult males (Figs. 1 and 2). Young lizards, however, tended to merge bobs 3 and 4 to a varying extent (Fig. 5). The percentage of displays in which these bobs were merged fell sharply through ontogeny, from 68% in Weekgroup 0.5 to 4% in Weekgroup 100 (Table 3).

In addition to deviations in the pattern of bobs 3 and 4 and the B Display characteristics described by Rothblum and Jenssen (1978), other pattern deviations were occasionally seen in both A and B Displays (Fig. 6). The most common of these was a bob with a step or "shoulder" (Fig. 6); these were observed with similar frequency in all Weekgroups (Table 3).

Changes in Unit Durations. Many bob and pause durations increased or decreased slightly during the time the lizards were video taped; however, duration shifts were not observed for all units nor for all lizards. For both A and B Displays, most units in the core pattern lengthened slightly between Agegroups, while interbob pauses following the core pattern (Units 8, 10, and 12) shortened (Figs. 7 and 8). Most unit duration changes between Agegroups ranged from 2% to 20% (Table 7). Core Duration (Table 1) lengthened through time, especially between Agegroup 2 and Agegroup 3; Post-Core Duration (Units 8-12 measured as a whole) shortened, especially between Agegroup 1 and Agegroup 2 (Fig. 9).

Several other methods were used to assess the amount of change in unit durations through time. First, a Variance Components Analysis (Barr, et. al., 1979) was used to break down the variance in unit durations into the proportions attributable to the independent variables Clutch, Individual, Weekgroup, and Error (Table 8). Weekgroup represents the relative amount of variance due to ontogeny, and Error represents largely the relative amount of variance due to intra-individual differences. The dependent variables used in this analysis were the means--computed for each Lizard, Weekgroup, and Display Type--of Total Bobs, Core Duration, and the durations of units 1-12. For example, one dependent variable was the mean of all Unit 3 durations which were performed by Lizard 35, at Weekgroup 2, of Display Type B.

The Variance Components Analysis revealed that of the total variance in unit durations, only 7.0 ± SD 7.0% for A Displays and 6.0 ± SD 4.0% for B Displays was attributable to Weekgroup (Table 8 and Appendix IV). These figures are the means of the 12 separate Variance Components estimates for each of Units 1-12. Thus, only 7% and 6% of total variance in A and B Display unit durations, respectively, could be attributed to ontogeny (Weekgroup). Weekgroup appears to account for a greater proportion of the variance when the seven units of the core pattern are treated as a whole (Core Duration): 20% of the variance in A Displays and 25% in B Displays (Table 8). For Total Bobs, Weekgroup accounts for 21% of the variance in A Displays and 31% in B Displays.

In contrast to the small proportion of variance attributed to ontogeny (Weekgroup), the total among lizards variance component was high (Table 8: 54% for A Displays, 51% for B Displays). Consequently, further analyses of ontogenic change were performed separately for individual lizards so that the relatively small effect of ontogeny would not be confounded by the large genetic effect of the differences among lizards.

In order to visualize the changes in unit durations for individual lizards, the data points for duration of Units 1-7 and of Core Duration were plotted against Age in Days. This was done only for lizards having a consistently large number of recorded displays through time (11 lizards for A Displays, 5 for B Displays); thus, for A Displays there were 77 plots (11 lizards X 7 units) for unit durations and 11 plots for Core Duration; for B Displays there were 35 plots (5 lizards X 7 units) for unit durations and 5 plots for

Core Duration. These plots (Appendix II) showed that the change in unit durations through time was roughly linear, with few abrupt changes. The only exception was lizard 35 which, at 8 weeks of age, abruptly shortened the durations of Unit 5 of its A Display and of Units 2 and 5 of its B Display. After 8 weeks the durations of these units also increased gradually through time.

For most lizards' units, Age in Days did not have a statistically significant effect on unit durations, as seen from linear regressions of unit durations against Age in Days (computed for the same group of lizards discussed above). Sixty-two percent of the 77 regressions for A Display unit durations and 76% of the 35 regressions for the B Display unit durations did not significantly deviate from a zero slope ($P > 0.05$; Table 9). The 38% of regressions of A Display units in which Age in Days did have a significant effect included 30% in which the slope was above zero and 8% in which the slope was below zero. The 24% of regressions of B Display units in which Age in Days had a significant effect included 17% in which the slope was above zero and 7% in which the slope was below zero (Table 9). For both A and B Displays, the unit showing the most change through time was Unit 4, which significantly lengthened with age in 10 of the 11 lizards for A Displays and in 4 of the 5 for B Displays. The Core Duration significantly lengthened with age in 8 of the 11 lizards for A Displays and in 4 of the 5 for B Displays (Table 9).

Visual comparisons of these regression lines among individuals were made from graphs, with the regression lines for all lizards drawn on the same coordinates; these graphs were made for Units 1-7 and for the Core Duration for A and B Displays (Appendices III, IV, and V). They showed the amount and direction of ontogenic change in unit duration for each individual as well as the magnitude of inter-individual differences. They provided a visual confirmation of the result shown by the Variance Components Analysis; i. e., that individual differences were much greater than ontogenic changes.

Changes in Stereotypy of Unit Durations. Throughout the study, the lizards performed A and B Displays whose unit durations were quite stereotyped both intra-individually and inter-individually. To show this, the Coefficient of Variation (C. V. = S.D. / Mean X 100) was used as a measure of stereotypy: the smaller the C. V. value, the less the variance and the greater the stereotypy. Almost all C. V. values for unit durations of A and B Displays fell within or below the 15-35% range reported by Barlow (1977: 103) as characteristic of many stereotyped behaviors.

Even with all 554 Type A Displays, and all 389 Type B Displays, pooled across individuals and across Agegroups, most C. V. values fell within Barlow's range. For units 1-12 of the pooled A Displays, the C. V. averaged 28%, ranging from 13% for Unit 3 to 68% for Unit 6, which was the shortest unit (Table 10). The C. V. of the Core Duration for all 554 A Displays was 11.4%. For units 1-12 of the B Displays, the C.V. averaged 29%, ranging from 14% for Unit 4 to 48% for Unit 6 (Table 11). The C. V. of the B Display Core Duration was 10.4%.

In order to make a distinction between intra-individual stereotypy (i. e., consistency of each individual's unit durations) and inter-individual stereotypy (i. e., consistency of unit durations from one individual to another), the 554 A Displays and 389 B Displays were sorted and averaged by individuals and then treated statistically in two different ways. Both provided a percentage measure (Coefficient of Variation) of stereotypy; however, they are not necessarily inter-comparable.

Intra-individual stereotypy was assessed by calculating the Coefficients of Variation for each unit of a lizard's displays. For a given unit, these within lizard C. V.s were next averaged; this mean C. V. estimates how stereotyped each unit was, on the average, within lizards (Tables 10 and 11, Column B). Unit 4 of both the A and B Displays was the most stereotyped (mean C. V. = 8% and 11%, respectively), while Unit 6 was the least stereotyped (mean C. V. = 38% and 34%, respectively (Tables 10 and 11, Column B).

Intra-individual stereotypy of unit durations and Core Duration did not change over time. Average stereotypy within lizards was very similar in Agegroups 1, 2, and 3 (Table 12). Even displays performed within the first two days were almost as intra-individually stereotyped as the displays of older lizards. One lizard performed 21 A Displays on its hatching day, with an average C. V. for Units 1-7 of 18% (Table 13).

To assess inter-individual stereotypy, the durations of each unit for each lizard were first averaged. Thus with a sample size of 34 lizards, there were 34 mean values for each unit. Next a mean of these 34 means was calculated for each unit and a C. V. derived, which estimated how stereotyped each unit was among lizards. For A Displays these C. V.s ranged from 10% for Unit 3 to 59% for Unit 6 (Table 10, Column C); for B Displays they ranged from 13% for Unit 4 to 43% for Unit 6 (Table 11, Column C).

Inter-individual stereotypy of unit durations and Core Duration also did not change over time for either A or B Displays. At Agegroups 1, 2, and 3, the average among lizard C. V.s for Units 1-7 of A Displays were 24%, 25%, and 23%, respectively; for B Displays they were 27%, 24%, and 27% (Table 14). This result can also be seen graphically on the plots of the linear regression lines of unit durations against Age in Days (Appendices III, IV, and V): regression lines for individuals do not converge toward a common value for the population.

### Individual Differences in Unit Durations

Slightly more than half of all variance in unit durations, for both A and B Displays, was attributed by the Variance Components Analysis to inter-individual differences (Table 8). Fifty-four percent of the variance in Units 1-12 for A Displays, and 51% for B Displays, was due to the among lizard component. The among lizards C. V.s provide another measure of inter-individual differences in unit durations. For Units 1-12, the average C. V. among lizards is 23% for A Displays and 26% for B Displays (Table 10 and 11).

## Individual Differences in Display Patterns

Many lizards performed B Displays with pattern deviations such as deleted Bob 1, deleted Bob 5, a dip preceding the fourth bob, or dips preceding the terminal bobs. However, individuals were not always consistent in their B Display patterns. End dips were featured in 92% (24/26) of the B Displays of one lizard and in 40% (6/15) of the B Displays of another. Four other lizards performed only one B Display with end dips (out of sample sizes of 3, 5, 9, and 12). Twenty-five lizards performed some B Displays with a dip preceding bob 4, but only three of these featured this dip in all of their B Displays (sample sizes 3, 4, and 5). Eighteen lizards eliminated bob 5 in some of their B Displays, but again, none was completely consistent in this. Five individuals deleted the first bob of some of their B Displays; they did so in 33% (2/6), 69% (11/16), 3% (1/30), 29% (2/7), and 67% (2/3) of their B Displays. In summary, I could not in every case draw a DAP graph for B Displays that was characteristic for a particular lizard.

There was often a graded expression in these pattern deviations; for instance, the first bob of the B Displays of one lizard was either normal, of extremely low amplitude, or totally absent. In some displays, dips preceded some of the terminal bobs but not others (this was scored as presence of dips).

A few lizards even exhibited occasional pattern deviations in their A Displays, a condition not observed in adult males by Rothblum and Jenssen (1978). Lizard 58, which performed end dips in 92% of its B Displays, also included them in 24% (6/25) of its A Displays. Four other A Displays, from 3 lizards, included end dips. A dip preceding bob 4 was found in at least one A Display of 12 individuals. No bob deletions, however, were observed in any A Displays.

### Sex Differences in Unit Durations

For both A and B Displays, males and females were very similar in their mean values of unit durations, Core Duration, and Total Bobs. The only variable which differed significantly (P = 0.03, T Test) by sex was Unit 6 of B Displays; it averaged 0.087 s for females and 0.063 s for males.

### Heritability of Display Parameters

Display behavior of S. u. hyacinthinus appears to have a high heritability. The among clutch variance components (a subset of the total between-lizards component) for unit durations averaged 30% for A Displays and 19% for B Displays (Table 8). Assuming that all clutchmates were full siblings, heritability estimates of unit durations averaged .60 = (.30 X 2) for A Displays and .38 = (.19 X 2) for B

Displays. The heritability estimates of the Core Duration were .80 for A Displays and 0 for B Displays, while those for Total Bobs were .66 for A Displays and .50 for B Displays. For A Displays, there was more variance among clutches (30%) than within clutches (24%), while for B Displays there was less variance among clutches (19%) than within clutches (32%) (Table 8).

There was little uniformity among clutches in the presence of B Display pattern deviations (e. g., Bob 4 dip, end dips, deleted Bob 1, and deleted Bob 5. For example, lizards in 6 of the 8 clutches featured a Bob 4 dip in some of their B Displays; among these clutches the percentage of all B Displays featuring this dip ranged from 12% to 78% (Table 15). The single B Display deviation which seemed to be clutch-specific was end dips; it appeared in 62% of the 54 B Displays of one clutch, yet was almost completely absent in the B Displays of the other clutches (Table 15).

## Miscellaneous Observations

Social Behavior. Within their enclosures, hatchlings were quite gregarious, often basking on the same perch and sleeping in the same shelter in physical contact; their social interactions did not appear to reflect either territoriality or dominance. Their tendency toward gregariousness seemed to go beyond the space limitations imposed by the size of the cages. Licking of other hatchlings was quite common, and often preceded or followed a display. Displays were often given in an assertion (i. e., non-directed) context, but even those which were clearly directed towards another hatchling did not usually appear to be performed in an aggressive manner. In contrast to behavior observed in adults, biting, tail lashing, and chasing occurred very infrequently among hatchlings. Prolonged volleys of displays were also infrequent, and most of those that were observed did not seem to have agonistic intent. In one prolonged interaction between one-week-old hatchlings, one displayed several times to another, which did not respond. The displaying lizard repeatedly ran off a short distance, then returned from another angle to display again to the other hatchling, lick it, and tilt its head at an angle toward the other. The recipient of the directed displays, partly hidden in a knothole, watched the displayer but did not display or leave the knothole.

In another, similar interaction between one-day-old hatchlings, one individual was again very active, leaving and returning several times and frequently licking the second hatchling on the snout or head before or after a display. The second hatchling did not display, but remained stationary for several minutes and then ran off.

In contrast to displays of hatchlings, displays of older lizards, especially males, in my study were sometimes clearly aggressive, were frequently directed at another lizard, and were sometimes followed by vigorous chasing, tail lashing, and open-mouthed lunging. The context for such displays was probably territorial, especially since the most aggressive displays were usually directed between large males. Older males also performed some displays in a courtship context. Both A and B Displays, interspersed with jiggles, were used in courtship. In response to male courtship, some adult females performed a distinctive "rejection display" (Carpenter, 1967), consisting of an arched back, raised tail, and sideways hunching movement, which had not been observed previously.

On several occasions, adult conspecifics occupied the same cage as hatchlings. The response of hatchlings after first seeing adults was usually to remain nearly motionless for several minutes and then to resume their usual activity. Hatchlings occasionally displayed to adults, but adults were not seen to respond in any way. Hatchlings appeared to be unafraid of adults and were sometimes in physical contact with them, as they were with other hatchlings; although new hatchlings were within the size range of prey taken by adults, none was ever eaten.

Food Preference. I observed in my lizards what appeared to be innate prey preferences similar to those reported for other lizards (e. g., Reznick et al., 1981, for

Sceloporus malachiticus, and Brockhusen, 1977 for Anolis lineatopus). Newly hatched lizards in my study were fed mostly field sweepings containing a variety of insects; innate prey preferences were indicated from informal observations of feeding behavior. No hatchling, including naive ones feeding for the first time, ever attempted to eat any Hymenopteran (with the possible exception of a few ants), even though small bees and wasps (less than 5mm) were usually present in the sweepings. Ladybird beetles (Coccinellidae) were always ignored by naive hatchlings, as were immature stinkbugs (Pentatomidae) and green lacewings (Chrysopidae), all of which are known to have an offensive odor or a noxious taste (Borror and White, 1970). Hard-bodied beetles and fuzzy caterpillars were never attacked. Of the prey eaten, the hatchlings had consistent preferences. House spiders (Theridiidae) were always seized instantly, often by more than one hatchling. Aphids, smooth-skinned caterpillars, and other very soft-bodied prey were singled out from other kinds of prey and quickly eaten. Leaf bugs (Miridae), on the other hand, were usually eaten after a long delay and with little enthusiasm.

Modal Action Patterns. There has been discussion (e. g. Barlow, 1977) of whether a Modal Action Pattern is always carried through to completion once it has been triggered, or whether it may be interrupted in response to external stimuli. *Sceloporus u. hyacinthinus* observed in this study did occasionally interrupt their displays in response to external stimuli. For example, on at least two occasions a lizard was displaying to another when the intended recipient ran off a short distance; the displaying lizard then broke off its display, ran around in front of the recipient and began another display from the beginning.

*Curiosity*. On several occasions, a novel object (for instance, an orange sphere about 7 cm diameter) was placed in a cage with hatchlings. The lizards usually remained still for 10-15 min, after which some of them slowly approached the object, often retreating and approaching again from a different angle. They sometimes tilted their heads at an angle towards the object, sometimes licked it, and at least one lizard displayed at the novel object. This behavior continued for 10-15 min.; thereafter, the lizards habituated to the novel object.

# Discussion

## Ontogenic Change

### Changes in the Form of Displays.

Both Type A and Type B Displays of *Sceloporus undulatus hyacinthinus* were present from the day of hatching and experienced little ontogenic change in the duration of display units or overall pattern. From a few hours or even minutes after hatching, some lizards performed both Type A and Type B Displays that were very similar to adult displays. Some hatchling displays differed slightly by having lower bob amplitude, fewer total bobs, a rounded appearance of the bobs, or incomplete separation between bobs 3 and 4; however, these characteristics were also seen at times in adult displays (Table 3) and appeared to be associated with a low level of arousal.

The frequency of these hatchling display characteristics diminished gradually, with no abrupt changes in display pattern. For example, half of the displays given in the first two days contained only two or three bobs, stopping short of completing the core pattern; after the first two days, incomplete displays became much less frequent, and the total number of bobs per display continued to increase throughout the study. A gradual refinement was also seen in the degree of separation between bobs 3 and 4 (Table 3).

The slight ontogenic changes in unit duration were not statistically significant in most cases (Table 9) and accounted for only 7% and 6%, respectively, of the total variance in the units of A and B Displays (Table 8). Further indication that unit durations changed very little during ontogeny is shown in the similarity of mean A Display unit durations, pooled across time, with the mean A Display unit durations found by Rothblum and Jenssen (1978) for adult males from the same population (Table 16).

The expectation that there might be more inter-individual or intra-individual variability among hatchlings than among older lizards was not borne out. Each individual was as variable in its unit durations in Agegroup 3 as it was in Agegroup 1 (Table 12); similarly, there was as much variability from one lizard to another in Agegroup 3 as there was in Agegroup 1 (Table 14).

These results agree with other observations of ontogenic change in lizard displays. Stamps (1978) found greater inter-individual variability in juveniles than in adults in only one of three display patterns of Anolis aeneus. As was the case in my study, Stamps (1978) also found intra-individual stereotypy to be the same in juveniles as in adults, and she found the only ontogenic change in display form to be a slight lengthening of the signature bob. Jenssen (1971) reported that displays of some adult Anolis nebulosus lengthened slightly after a year's interval.

Behaviorists now believe it is largely unproductive to label a particular behavior as "innate" or "learned" (Tooker and Miller, 1980; Burghardt, 1977; Hailman, 1967). Rather, most behaviors are affected by both genetic and experiential factors plus the interaction between them. There are many examples of interaction between a predisposition to behave in a certain way, and learning (Bateson, 1981). For example, the initial prey preferences of some snakes are readily modified by experience (Burghardt, 1970).

Alcock (1979), in consideration of these interactions, refined the innate/learned dichotomy by proposing a continuum ranging from closed instincts and open instincts to closed learning and open learning. An example of a closed instinct would be the courtship movements of male spiders; these movements must be perfect on first performance, lest the spider become a meal for its prospective mate. Open instincts would include the innate prey preferences of snakes (Burghardt, 1970) and the innate food-begging behavior of gull chicks, which is refined and perfected through experience (Hailman, 1967).

The display patterns of S. u. hyacinthinus appear to be near the "closed instinct" end of Alcock's (1979) continuum. Of the several factors (e. g., genotype, maturation, hormones, sensitive periods, reinforcement, habituation, learning, and insight) which Burghardt (1977) listed as being potential antecedents or modifiers of a communication behavior, only genotype appeared to be a major factor affecting display patterns of the lizards in my study.

A possible reason for the early stereotypy and relative absence of ontogenic change in lizard displays may be that lizards are precocial; everything that is needed for "successful" completion of display behavior (e. g., information in the central nervous system and the muscle system to carry out instructions) is present at hatching. Compared with gulls, lizards hatch at a later stage of neuro-muscular development.

Changes in Display Behavior. While very little ontogenic change was found in the A and B patterns themselves, somewhat more change was found in display behavior, or the ways in which the lizards utilized the display patterns. In display behavior I include display frequency, A:B ratio, context in which displays were performed, stimuli releasing displays, and the use of modifiers with displays. Of these, only the first two were quantified in this study.

Display frequency per hour of observation time increased between Agegroup 2 and Agegroup 3 for both sexes. For males the frequency doubled (Table 4), but the difference was not significant for either sex because of the large variance among individuals. I believe the increase in display frequency for males in Agegroup 3 to be biologically significant; the large standard errors among individual males may be due to establishment of dominance relationships during this Agegroup; there would then be a tendency for dominant males to display more frequently and for subordinate males to display less frequently. Establishment of dominance relationships may in turn be due to sexual maturation, since some lizards reached sexual maturity during Agegroup 3.

Another change in behavior which may have been due to maturation was a change in A:B ratio for females. For females in Agegroup 3, this ratio was significantly higher than that for all other males and females (Table 6). Although the difference in message content between A and B displays is not known, it is possible that the B Display indicates a more intense level of agonistic intent than does the A Display (Rothblum and Jenssen, 1978). Stamps (1978) found that female _A_. _aeneus_ showed a decreased frequency of aggressive displays with maturity.

Stimuli which induced displays and the contexts in which displays were given were not quantified in my study. However, during ontogeny the displays seemed gradually to be used in increasingly aggressive or territorial contexts or even in courtship; later displays were more often directed toward a cagemate and were sometimes followed by chasing, tail lashing, and occasionally biting.

Use of display modifiers (sensu Jenssen 1978) such as dorso-lateral flattening, gorged throat, and a stiff four-legged stance during displaying seemed to increase through time, and became especially noticeable in males which were at least 45 mm SVL and which had the blue coloration of the venter, a character of adult males.

The apparent absence of aggression, territoriality, courtship, or other context for the displays of hatchling *S. u. hyacinthinus* raises the question of their adaptive value. Display behavior of hatchlings of this species may possibly be viewed simply as practice for adult behavior. This impression was strengthened by observation of the very few prolonged display bouts between small hatchlings. Two such incidents were described on p. 24; both were characterized by a complete lack of aggression. It is possible, however, that *S. u. hyacinthinus* hatchlings are more aggressive and territorial under natural conditions than they appeared to be in captivity. Simon and Middendorf (1980) report that hatchling and juvenile *Sceloporus jarrovi* are territorial in the field. Stamps (1978) found that displays of hatchling *A. aeneus* served to establish and maintain territories; she also speculated that hatchling display behavior in this species might function in defense of future resources.

## Individual Differences

Differences among individuals in both A and B Display patterns were present at hatching and were maintained at the same level throughout ontogeny. Inter-individual differences in unit durations accounted for 54% and 51%, respectively, of the variance in unit durations for A and B Displays (Table 8). The finding that A Displays differed as greatly among individuals as B Displays was unexpected. Rothblum and Jenssen (1978), in their study of adult male *S. u. hyacinthinus* from the same population, found significant inter-individual variability in B Display units durations, but no corresponding differences in the units of A Displays.

For B Displays, Rothblum and Jenssen (1978) found inter-individual differences in the display pattern itself as well as in the unit durations. These included deviations such as deleted bobs and dips preceding some bobs. Some of the lizards in my study, both males and females, had a tendency to include one or more of these pattern deviations in their B Displays; however, my lizards were not always consistent in their B Display pattern, as was reported for adult males by Rothblum and Jenssen (1978). Because sample sizes were similar in the two studies (average number of B Displays per individual was 10.3 in the present study and 7.2 for Rothblum and Jenssen), the difference in results is unlikely to be due to sample size differences.

## Conclusion

The data presented here show that the ontogenic effect is relatively unimportant in the display patterns of *Sceloporus undulatus hyacinthinus*, and that the heritability of the display patterns is high. This would indicate that further studies of display patterns in this and closely related species could be carried out with either hatchlings or adults, with comparable results; nothing would be gained by maintaining hatchlings in captivity to mature size. Further study is needed to: (1) identify the differences in message content or context between Type A and Type B Displays; (2) determine whether context can be affected by environmental variables; and (3) to determine whether the Type B pattern deviations may aid in individual recognition.

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Table 1. Twenty-five variables used in the data analyses of each display. See Materials and Methods for details.

| Displayer Variables | Definition |
|---|---|
| 1) Identification number | Identification of individual lizard |
| 2) Hatching date | |
| 3) Clutch | The clutch from which a lizard came |
| 4) Sex | |
| 5) Age (of displayer) in Days | By subtraction of hatching date from date of display |
| Display Variables | |
| 6) Display Type | Type A or Type B |
| 7-18) Unit 1-12 Durations | See text for details |
| 19) Core Duration | Duration of display from start of first bob to end of fourth bob (Units 1-7) |
| 20) Post-Core Duration | Duration of display from start of Unit 8 through end of Unit 12 |
| 21) Keyratio | Unit 2 duration / Unit 3 duration |
| 22) Total bobs | Number of bobs in display |
| 23) Ratio | Amplitude of Bob 3 / Bob 4 (measured directly from each DAP graph) |
| 24) 3-4 Index | A scale rating the appearance of Bobs 3 and 4; see Fig. 7 |
| 25) Bob 4 Dip | Presence or absence of dip preceding bob 4 |
| 26) End Dips | Presence or absence of dips preceding terminal bobs |

Table 2. Three time classifications of displays. Age (in days) is the age of the lizard at the time the display was performed. The names of the Weekgroup categories are derived from the number of weeks at the endpoint of the corresponding Age in Days.

| Age (in days) | Weekgroup | Agegroup |
|---|---|---|
| 0 - 3 | 0.5 | 1 |
| 4 - 7 | 1 | |
| 8 - 14 | 2 | |
| 15 - 28 | 4 | 2 |
| 29 - 56 | 8 | |
| 57 - 140 | 20 | |
| 141 - 196 | 28 | 3 |
| 197 - 365 | 52 | |
| ≥ 366 | 100 | |

Table 3. Percentage of displays (Type A and Type B Displays combined) of *Sceloporus undulatus hyacinthinus* at each Weekgroup that feature (A) bobs that are rounded rather than squared; (B) third and fourth bobs that are merged or incomplete; and (C) one or more shouldered bobs. See text for explanation.

| Weekgroup | Rounded Bobs | Merged Third and Fourth Bobs | Shouldered Bobs |
|---|---|---|---|
| 0.5 | 68 | 49 | 10 |
| 1 | 49 | 16 | 11 |
| 2 | 36 | 16 | 13 |
| 4 | 31 | 11 | 9 |
| 8 | 10 | 18 | 5 |
| 20 | 11 | 9 | 11 |
| 28 | 4 | 5 | 2 |
| 52 | 10 | 0 | 4 |
| 100 | 4 | 2 | 17 |

Table 4. Number of Displays (either A or B) performed per hour of observation time at each Agegroup (mean among individuals ± SE) by *Sceloporus undulatus hyacinthinus*. No comparison is statistically significant ($P > 0.05$, Mann-Whitney U Tests).

| | Agegroup | | |
|---|---|---|---|
| | 1 | 2 | 3 |
| Males (10) | 2.87 ± 0.76 | 3.56 ± 1.06 | 7.15 ± 3.27 |
| Females (8) | 3.00 ± 1.07 | 3.01 ± 0.89 | 4.36 ± 1.65 |

Table 5. Mean ( ± 1 SE) of the individual means for total number of bobs per display, by Agegroup, for *Sceloporus undulatus hyacinthinus*. Number of lizards in parentheses. Asterisks denote significance at 0.001 level (Mann-Whitney U Tests).

| | *A Displays* | *B Displays* |
|---|---|---|
| *Agegroup 1* | 5.3 ± 0.36 (34) | 5.3 ± 0.31 (29) |
| | * | * |
| *Agegroup 2* | 7.0 ± 0.33 (34) | 7.2 ± 0.38 (24) |
| *Agegroup 3* | 7.4 ± 0.37 (22) | 8.5 ± 0.56 (19) |

Table 6. Ratio of A:B Displays, by Agegroup, pooled for male and for female *Sceloporus undulatus hyacinthinus* in each Agegroup. Two females that never performed B Displays were excluded from this analysis. Asterisks denote a significant difference ($P < 0.05$, Chi-square tests).

| | | Agegroup | | |
|---|---|---|---|---|
| | 1 | 2 | | 3 |
| Males | 1.28 | 1.23 | | 1.19 |
| | | | | * |
| Females | 1.86 | 1.59 | * | 3.32 |

Table 7. Means of individual mean unit durations (s) for Units 1-12 of A and B Displays, by Agegroup (AG), of *Sceloporus undulatus hyacinthinus*, and percent change from Agegroup 1 to Agegroup 2 and from Agegroup 1 to Agegroup 3.

| | AG 1 | AG 2 | Change From AG 1 | AG 3 | Change From AG 1 |
|---|---|---|---|---|---|
| *A Display* | | | | | |
| Units | | | | | |
| 1 | 0.24 | 0.27 | +11% | 0.31 | +28% |
| 2 | 0.33 | 0.34 | + 2% | 0.39 | +17% |
| 3 | 0.64 | 0.66 | + 4% | 0.70 | +10% |
| 4 | 0.73 | 0.76 | + 5% | 0.87 | +19% |
| 5 | 0.29 | 0.27 | - 6% | 0.30 | + 1% |
| 6 | 0.09 | 0.08 | -10% | 0.07 | -22% |
| 7 | 0.34 | 0.33 | - 3% | 0.39 | +14% |
| 8 | 0.38 | 0.33 | -14% | 0.32 | -17% |
| 9 | 0.23 | 0.25 | +11% | 0.26 | +14% |
| 10 | 0.41 | 0.38 | - 7% | 0.36 | -12% |
| 11 | 0.22 | 0.20 | -11% | 0.23 | + 4% |
| 12 | 0.45 | 0.41 | -11% | 0.39 | -13% |
| Core Duration | 2.64 | 2.72 | + 3% | 3.01 | +14% |
| Post-Core | 1.70 | 1.56 | - 8% | 1.56 | - 8% |
| *B Display* | | | | | |
| Units | | | | | |
| 1 | 0.16 | 0.18 | + 8% | 0.22 | +33% |
| 1 | 0.55 | 0.56 | + 2% | 0.59 | + 6% |
| 3 | 0.40 | 0.43 | + 6% | 0.49 | +23% |
| 4 | 0.98 | 1.01 | + 3% | 1.07 | + 9% |
| 5 | 0.19 | 0.20 | + 2% | 0.20 | + 4% |
| 6 | 0.09 | 0.07 | -22% | 0.07 | -20% |
| 7 | 0.31 | 0.31 | + 1% | 0.34 | +11% |
| 8 | 0.51 | 0.43 | -17% | 0.40 | -21% |
| 9 | 0.16 | 0.13 | -18% | 0.17 | + 2% |
| 10 | 0.53 | 0.43 | -17% | 0.39 | -26% |
| 11 | 0.13 | 0.13 | + 2% | 0.15 | +14% |
| 12 | 0.52 | 0.46 | -12% | 0.42 | -20% |
| Core Duration | 2.62 | 2.69 | + 3% | 2.96 | +13% |
| Post-Core | 1.85 | 1.58 | -12% | 1.53 | -17% |

Table 8. Summary of Variance Components Analysis (Appendix IV gives results for individual units), showing the percentage of total variance in 1) Units 1-12 (averaged), 2) the Core Duration, and 3) Total Bobs, for A and B Displays of Sceloporus undulatus hyacinthinus which was attributed to variance 1) among clutches, 2) among lizards within clutches, 3) among Weekgroups, and 4) within individuals.

| | Dependent Variables | | |
|---|---|---|---|
| Independent Variables | Units 1-12 (Mean ± SD) | Core Duration | Total Bobs |
| A Displays | | | |
| Total Among Lizards Component | 54 | 69 | 36 |
| (Among Clutches) | 30 ± 13 | 40 | 33 |
| (Among Lizards Within Clutches) | 24 ± 13 | 29 | 3 |
| Among Weekgroups | 7 ± 7 | 20 | 21 |
| Error | 39 ± 15 | 11 | 43 |
| Total | 100 | 100 | 100 |
| B Displays | | | |
| Total Among Lizards Component | 51 | 49 | 33 |
| (Among Clutches) | 19 ± 21 | 0 | 25 |
| (Among Lizards Within Clutches) | 32 ± 19 | 49 | 8 |
| Weekgroup | 6 ± 4 | 25 | 31 |
| Error | 43 ± 20 | 24 | 36 |
| Total | 100 | 100 | 100 |

Table 9. Number of lizards (*Sceloporus undulatus hyacinthinus*) whose regression line slopes are significantly (P < 0.05) and not significantly (P > 0.05) different from zero for regressions on age in days of Units 1-12 for A Displays of 11 lizards and of B Displays of 5 lizards whose displays were recorded from at least 0 to 325 days of age.

| | Number of Lizards (Total 11) | | |
|---|---|---|---|
| | Having (+) Slope | Having (-) Slope | Having No Slope (P>0.05) |
| **A Display** | | | |
| Units | | | |
| 1 | 4 | 1 | 6 |
| 2 | 7 | 1 | 3 |
| 3 | 6 | 0 | 5 |
| 4 | 10 | 0 | 1 |
| 5 | 2 | 2 | 7 |
| 6 | 2 | 2 | 7 |
| 7 | 4 | 1 | 6 |
| 8 | 0 | 1 | 10 |
| 9 | 1 | 0 | 10 |
| 10 | 1 | 1 | 9 |
| 11 | 0 | 0 | 11 |
| 12 | 1 | 1 | 7 |
| Core Duration | 8 | 0 | 3 |
| Post-Core | 0 | 1 | 7 |
| | Number of Lizards (Total 5) | | |
| **B Display** | | | |
| Units | | | |
| 1 | 0 | 0 | 5 |
| 2 | 1 | 1 | 3 |
| 3 | 1 | 0 | 4 |
| 4 | 4 | 0 | 1 |
| 5 | 0 | 0 | 5 |
| 6 | 1 | 0 | 4 |
| 7 | 2 | 0 | 3 |
| 8 | 0 | 2 | 3 |
| 9 | 0 | 0 | 5 |
| 10 | 0 | 0 | 5 |
| 11 | 0 | 0 | 5 |
| 12 | 0 | 1 | 4 |
| Core Durationn | 4 | 0 | 1 |
| Post-Core | 0 | 1 | 4 |

Table 10. Estimates of variability (expressed in Coefficients of Variation) for Units 1-12 of A Displays of _Sceloporus undulatus hyacinthinus_: for all A Displays pooled (A); for intra-individual variability (B); and for inter-individual variability (C). See text for explanation.

| | A<br>C. V. of all 554 A Dislpays | B<br>Mean of Lizards' C. V.s | C<br>C. V. of Lizard Means |
|---|---|---|---|
| _A Display_ | | | |
| Units | | | |
| 1 | 34 | 19 | 23 |
| 2 | 30 | 14 | 27 |
| 3 | 13 | 8 | 10 |
| 4 | 15 | 10 | 13 |
| 5 | 23 | 18 | 18 |
| 6 | 68 | 38 | 59 |
| 7 | 26 | 15 | 20 |
| 8 | 29 | 17 | 18 |
| 9 | 30 | 19 | 28 |
| 10 | 20 | 12 | 17 |
| 11 | 30 | 17 | 31 |
| 12 | 19 | 12 | 15 |
| Average of Units 1-12 | 28 | 17 | 23 |
| Core Duration | 11.4 | 5.3 | 9.4 |

Table 11. Estimates of variability (expressed in Coefficients of Variation) for Units 1-12 of B Displays of _Sceloporus undulatus hyacinthinus_: for all B Displays pooled (A); for intra-individual variability (B); and for inter-individual variability (C). See text for explanation.

| | A | B | C |
|---|---|---|---|
| | C. V. of All 389 B Displays | Mean of Lizards' C. V.'s | C. V. of Lizard Means |
| _B Display_ | | | |
| Units | | | |
| 1 | 46 | 25 | 36 |
| 2 | 23 | 10 | 24 |
| 3 | 22 | 12 | 23 |
| 4 | 14 | 9 | 13 |
| 5 | 25 | 20 | 27 |
| 6 | 48 | 34 | 43 |
| 7 | 19 | 12 | 17 |
| 8 | 29 | 15 | 29 |
| 9 | 38 | 25 | 41 |
| 10 | 19 | 13 | 17 |
| 11 | 41 | 23 | 30 |
| 12 | 21 | 14 | 14 |
| Average of Units 1-12 | 29 | 18 | 26 |
| Core Duration | 10.4 | 5.0 | 8.7 |

Table 12. Mean of lizards' Coefficients of Variation (an estimate of intra-individual variability), by Agegroup, for Units 1-7, Core Duration, and Total Bobs of A and B Displays of *Sceloporus undulatus hyacinthinus*.

| | Agegroup | | |
|---|---|---|---|
| | 1 | 2 | 3 |
| A Display | | | |
| Units | | | |
| 1 | 17 | 13 | 16 |
| 2 | 13 | 13 | 12 |
| 3 | 7 | 7 | 6 |
| 4 | 8 | 12 | 8 |
| 5 | 10 | 11 | 13 |
| 6 | 41 | 59 | 36 |
| 7 | 11 | 14 | 10 |
| Core Duration | 3.7 | 5.0 | 3.1 |
| Total Bobs | 25 | 29 | 21 |
| B Display | | | |
| Units | | | |
| 1 | 28 | 22 | 21 |
| 2 | 8 | 7 | 7 |
| 3 | 10 | 13 | 8 |
| 4 | 6 | 10 | 5 |
| 5 | 60 | 30 | 18 |
| 6 | 49 | 41 | 35 |
| 7 | 13 | 8 | 13 |
| Core Duration | 3.8 | 5.1 | 4.1 |
| Total Bobs | 25 | 22 | 19 |

Table 13. Coefficients of Variation for Units 1-7 (averaged) of the A Displays performed by two <u>Sceloporus undulatus hyacinthinus</u> at 0, 1, and 2 Days of Age. Number of displays in parentheses.

| Lizard I. D. | Age | C. V. | (N) |
|---|---|---|---|
| 77 | 0 | 18 | (21) |
| 77 | 1 | 24 | (10) |
| 88 | 1 | 24 | (20) |
| 88 | 2 | 15 | ( 7) |

Table 14. Coefficients of Variation of lizard means (an estimate of inter-individual variability), by Agegroup, for Units 1-7, Core Duration, and Total Bobs for A and B Displays of _Sceloporus_ _undulatus_ _hyacinthinus_.

| | Agegroup | | |
|---|---|---|---|
| | 1 | 2 | 3 |
| _A_ _Displays_ | | | |
| Units | | | |
| 1 | 26 | 26 | 16 |
| 2 | 27 | 29 | 26 |
| 3 | 10 | 10 | 9 |
| 4 | 14 | 13 | 12 |
| 5 | 20 | 17 | 16 |
| 6 | 53 | 62 | 63 |
| 7 | 18 | 18 | 20 |
| Mean of Units 1-7 | 24 | 25 | 23 |
| Core Duration | 10 | 11 | 8 |
| Total Bobs | 39 | 27 | 22 |
| _B_ _Display_ | | | |
| Units | | | |
| 1 | 41 | 36 | 30 |
| 2 | 23 | 24 | 25 |
| 3 | 26 | 16 | 28 |
| 4 | 16 | 13 | 9 |
| 5 | 35 | 21 | 25 |
| 6 | 29 | 38 | 60 |
| 7 | 21 | 17 | 13 |
| Mean of Units 1-7 | 27 | 24 | 27 |
| Core Duration | 11 | 9 | 6 |
| Total Bobs | 29 | 25 | 28 |

Table 15. Percentage of B Displays featuring Bob 4 Dip, End Dips, deleted Bob 1 (No Bob 1), and deleted Bob 5 (No Bob 5), by clutch, for *Sceloporus undulatus hyacinthinus*.

| Clutch I. D. | Indivs. (N) | Displays (N) | Bob 4 Dip | End Dips | No Bob 1 | No Bob 5 |
|---|---|---|---|---|---|---|
| 10 | 5 | 45 | 64 | 2 | 0 | 24 |
| 20 | 2 | 14 | 0 | 0 | 0 | 14 |
| 30 | 10 | 140 | 44 | 1 | 0 | 4 |
| 50 | 5 | 54 | 61 | 62 | 28 | 11 |
| 62 | 1 | 33 | 12 | 0 | 0 | 0 |
| 70 | 5 | 36 | 78 | 0 | 7 | 27 |
| 80 | 5 | 16 | 63 | 0 | 14 | 31 |
| 90 | 3 | 13 | 0 | 0 | 0 | 0 |

Table 16. Mean unit durations of A Displays for 11 adult males (Rothblum and Jenssen, 1978) and of all A Displays in my study (pooled across time). Sample sizes in parentheses. An adjustment was made to allow for the difference between the two studies in measurement technique.

| Unit | Rothblum and Jenssen | | Present Study | |
|---|---|---|---|---|
| 1 | 0.230 | (98) | 0.267 | (506) |
| 2 | 0.332 | (98) | 0.348 | (525) |
| 3 | 0.663 | (98) | 0.657 | (540) |
| 4 | 0.857 | (98) | 0.793 | (531) |
| 5 | 0.315 | (98) | 0.297 | (513) |
| 6 | 0.062 | (98) | 0.071 | (449) |
| 7 | 0.360 | (98) | 0.357 | (454) |
| 8 | 0.318 | (98) | 0.329 | (392) |
| 9 | 0.250 | (98) | 0.249 | (370) |
| 10 | 0.375 | (98) | 0.373 | (285) |
| 11 | 0.202 | (98) | 0.224 | (267) |
| Core Duration | 2.79 | (98) | 2.82 | (416) |

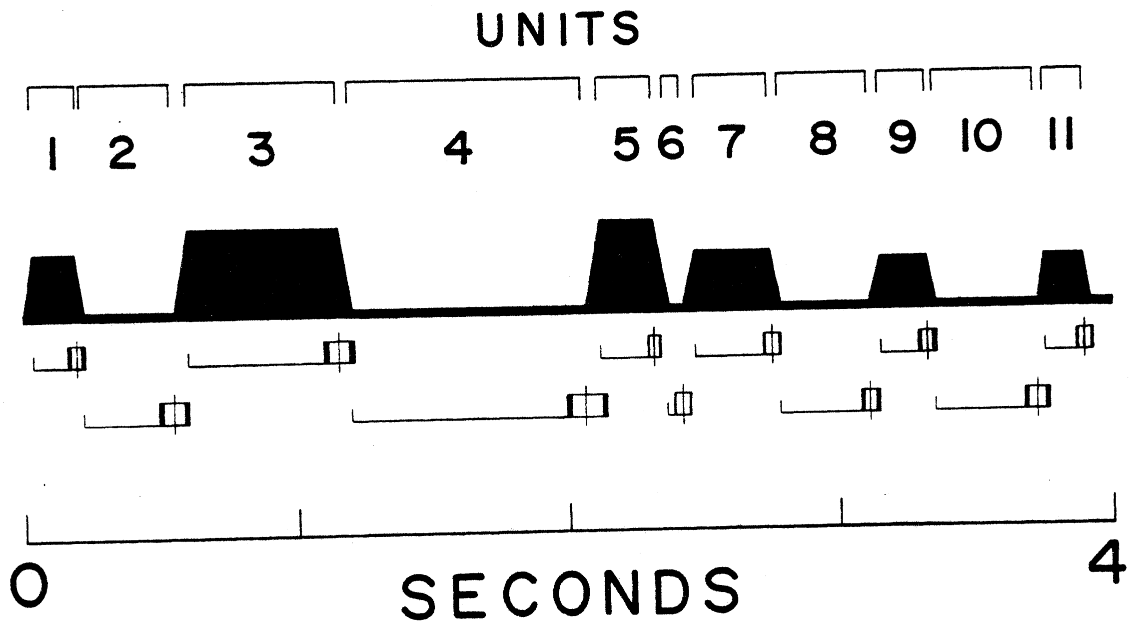


Fig. 1. The typical Type A display pattern of adult male Sceloporus undulatus hyacinthinus. To facilitate analysis, the display has been divided into units. Outer edges of white and black boxes represent 95% and 99% confidence intervals, respectively. After Rothblum and Jenssen (1978).

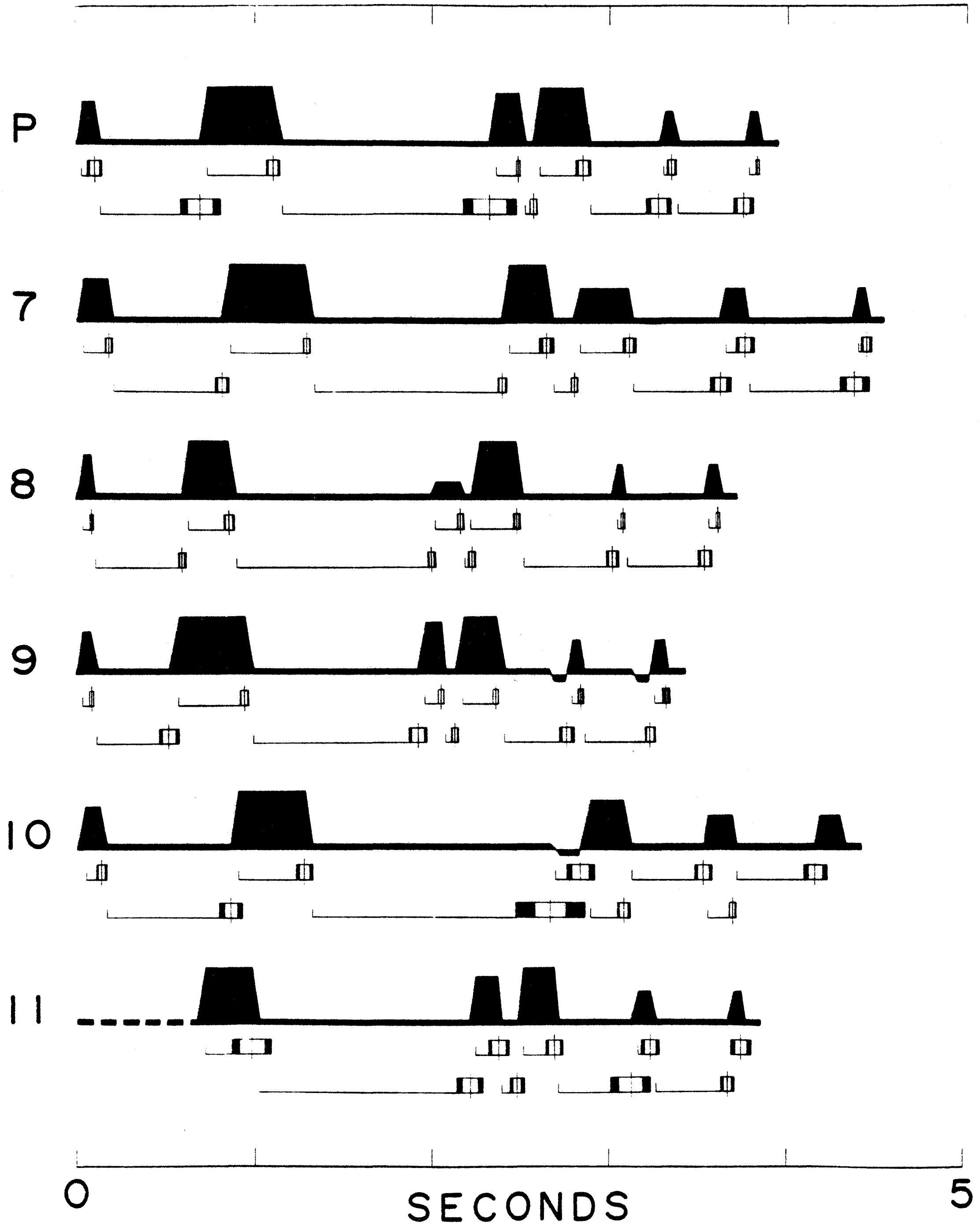


Fig. 2. The pooled Type B display pattern performed by 6 of the 11 adult male Sceloporus undulatus hyacinthinus in Rothblum and Jenssen's 1978 study (P); the five individually-unique Type B patterns performed by the remaining males (7-11). After Rothblum and Jenssen (1978).

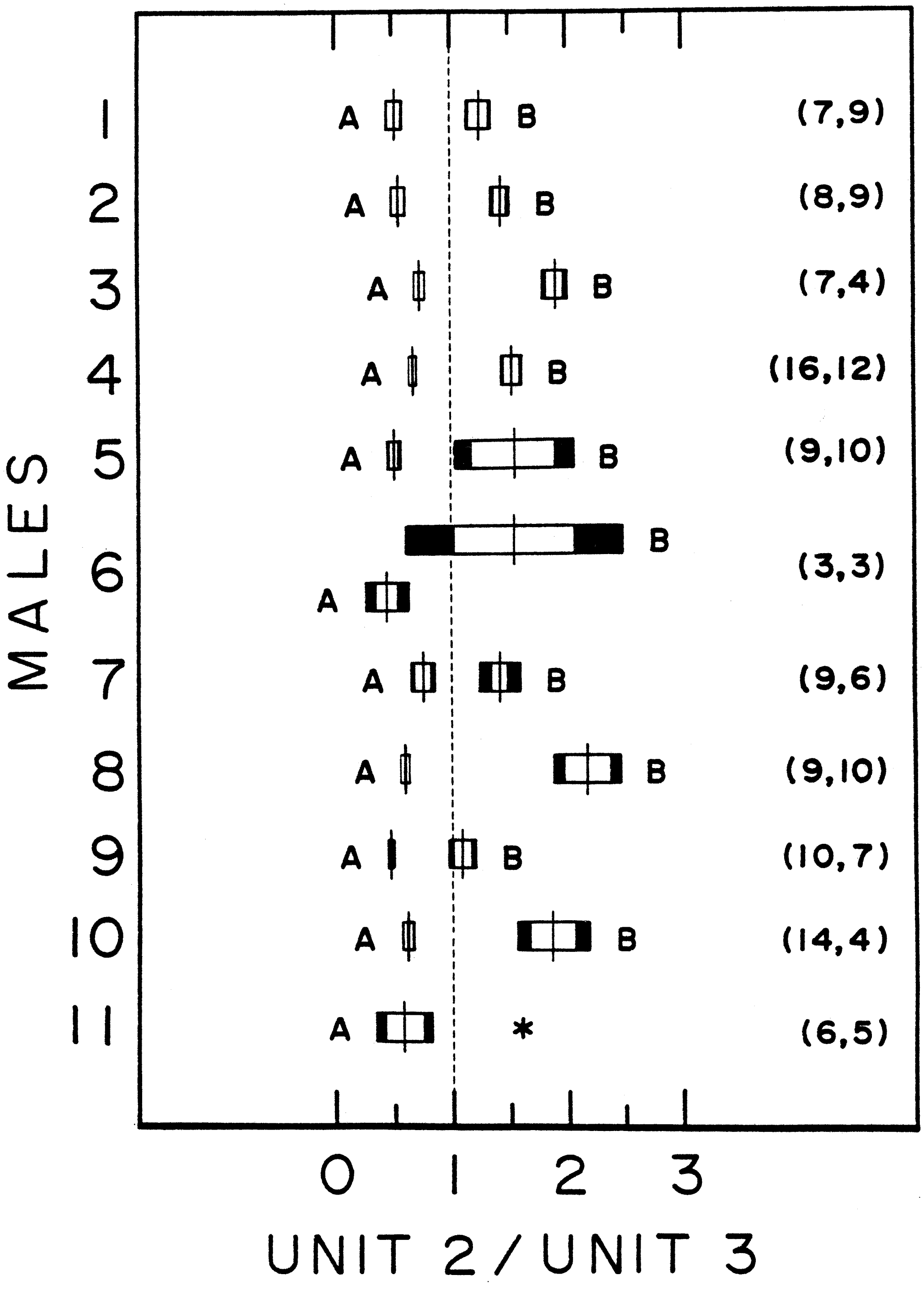


Fig. 3. Mean values of the Unit 2 / Unit 3 duration ratio for both A and B Displays of the 11 adult male *Sceloporus undulatus hyacinthinus* in Rothblum and Jenssen's 1978 study. The dotted line, representing a Unit 2 / Unit 3 duration ratio of 1.0, discriminates between the A and B Displays in almost all cases. The star represents a male who had no Unit 2 in his B Displays.

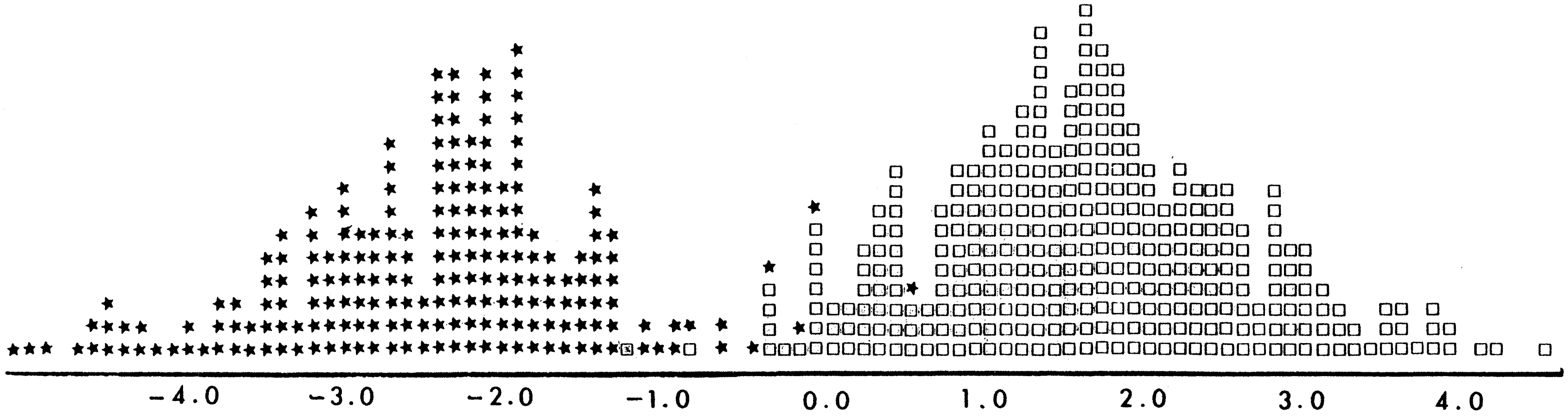


Fig. 4. The distribution of Type A (squares) and Type B (stars) displays of *Sceloporus undulatus hyacinthinus* as apportioned by a Discriminant Function Analysis (Jenrich and Sampson, 1979). The horizontal axis is a scale of the values of solutions to a function using the variables: durations of Units 1, 2, 3, 4, 7, and 9; Ratio; and Keyratio. Note the strongly bimodal distribution of the display types and the almost complete separation between them.

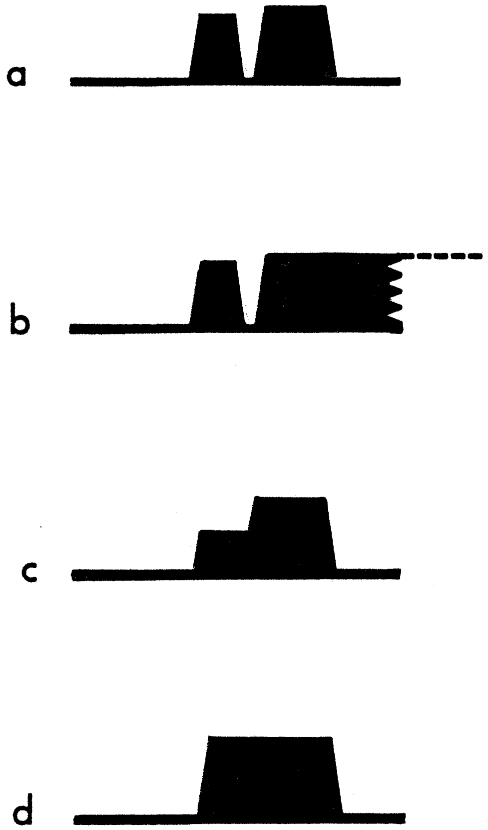


Fig. 5. Four forms of Bobs 3 and 4 that were observed at times in both Type A and Type B Displays of *Sceloporus undulatus hyacinthinus*. Complete separation of the bobs (a) is the normal pattern. In (b), the lizard's head fails to descend from Bob 4. (c) is a single "stepped" or shouldered bob. In (d) there is a single, long bob rather than two shorter bobs.

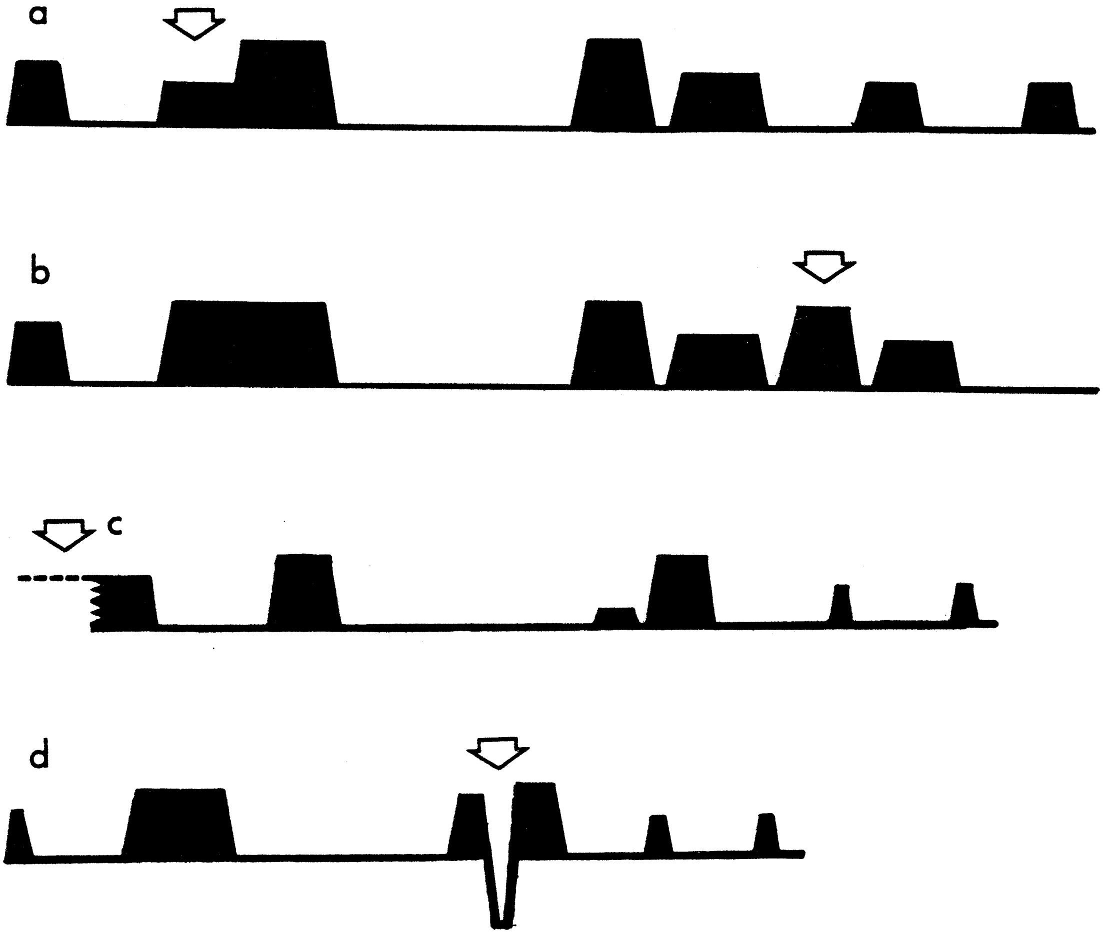


Fig. 6. Four examples of deviant display patterns occasionally observed in displays of *Sceloporus undulatus hyacinthinus*. (a) shows a display with a shouldered bob, which was the most common deviation. Shoulders appeared on any bob and on either side of the bob in both A and B Displays. (b) shows the apparent repetition of the third and fourth bobs. this appeared in only a few displays of one individual. In (c) the initial head movement is descending rather than ascending; this was seen in a small number of B Displays. (d) shows an exaggerated dip between bobs 3 and 4.

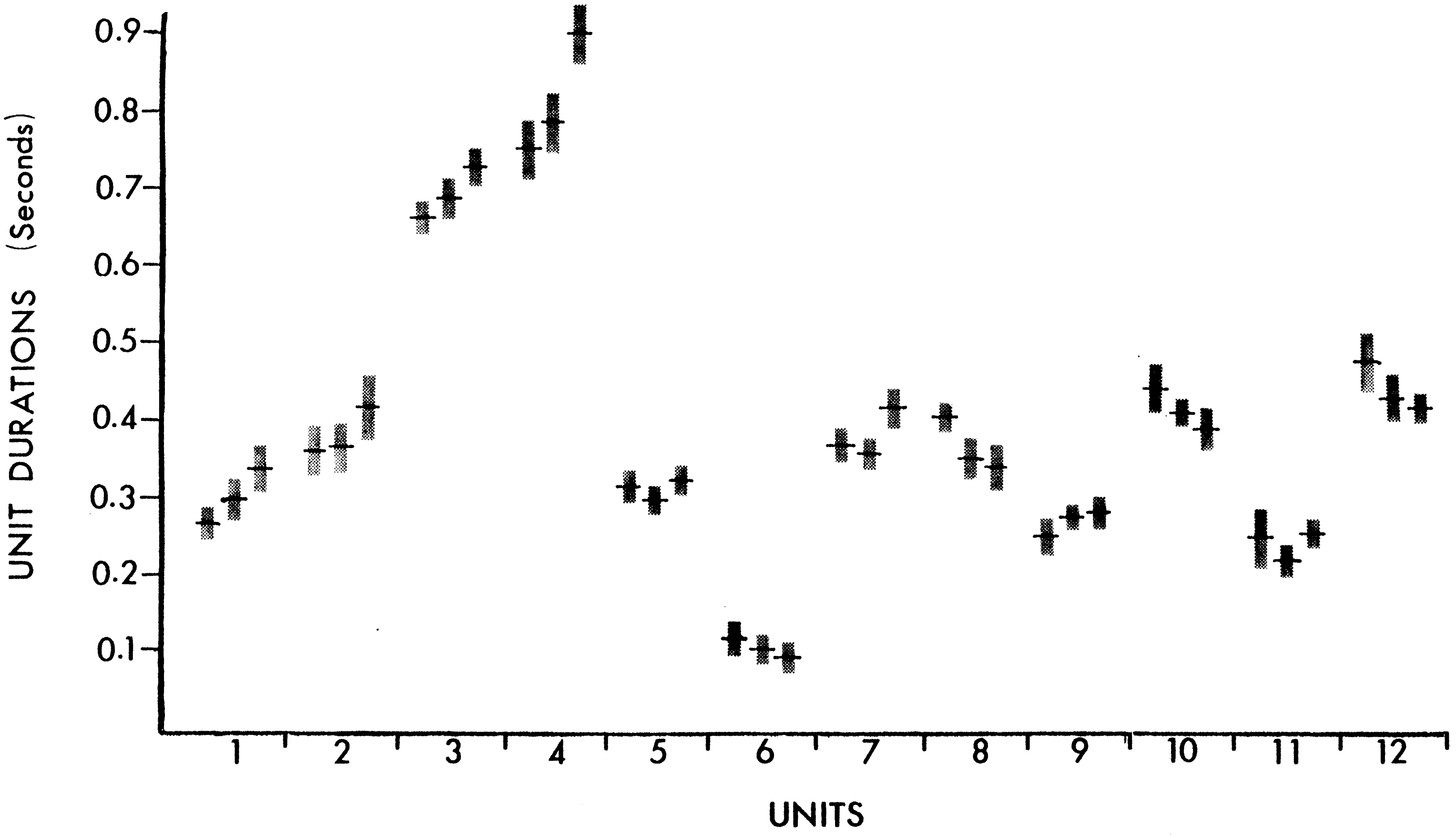


Fig. 7. For A Displays, the mean and 95% confidence intervals for durations of Units 1-12 at Agegroups 1, 2, and 3. These are the means of the individual lizard means.

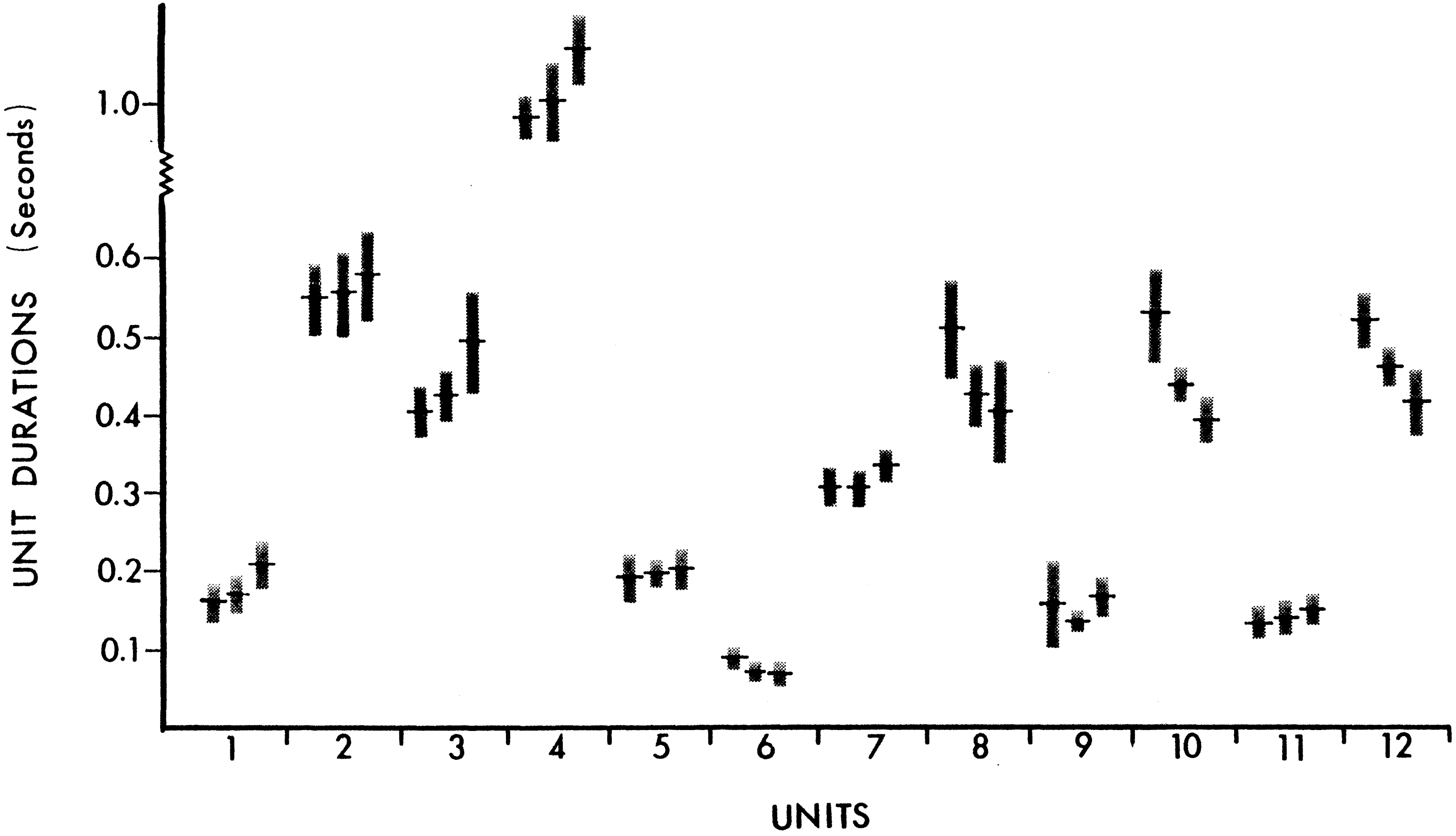


Fig. 8. For B Displays, the mean and 95% confidence intervals for durations of Units 1-12 at Agegroups 1, 2, and 3. These are the means of the individual lizard means.

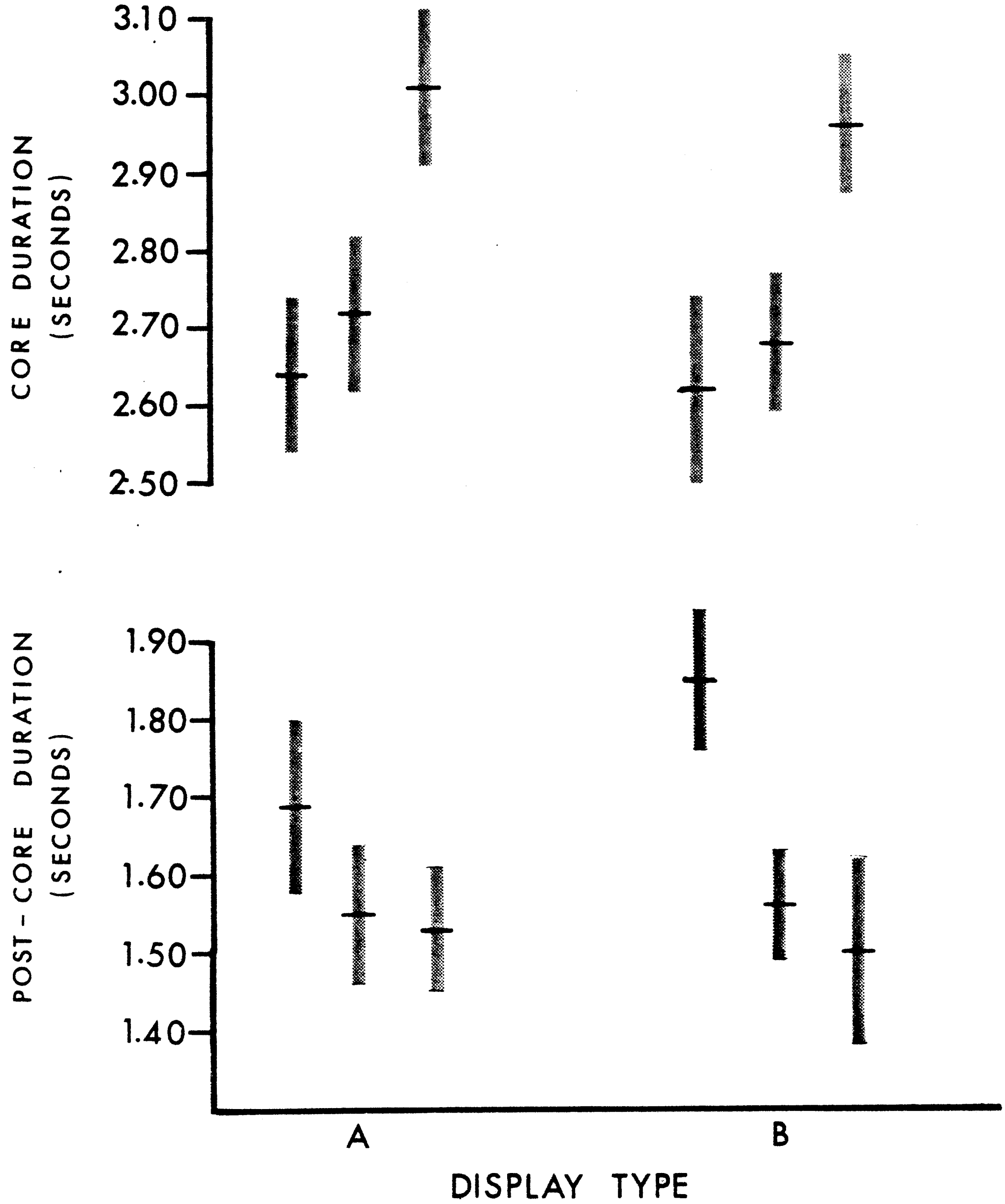
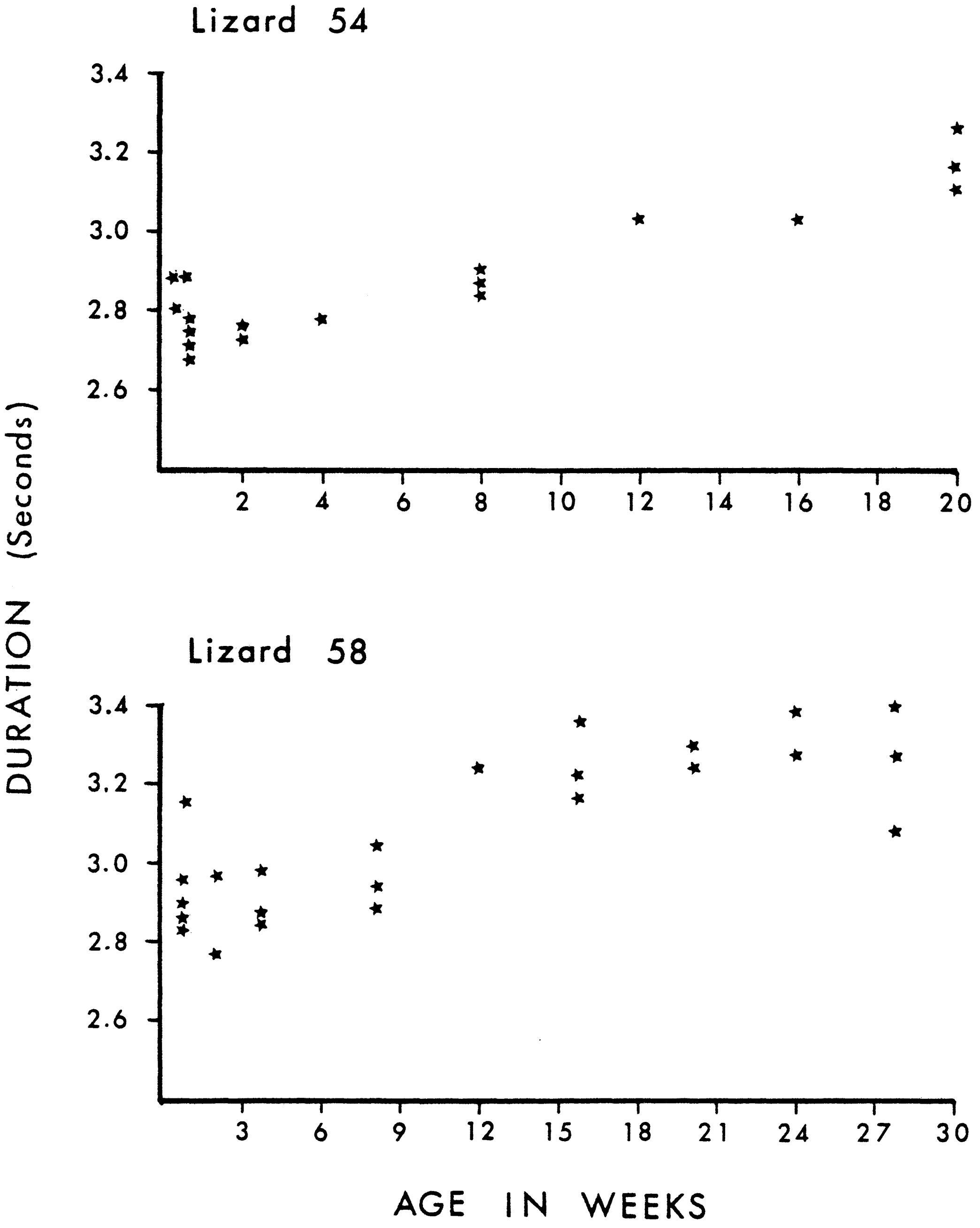


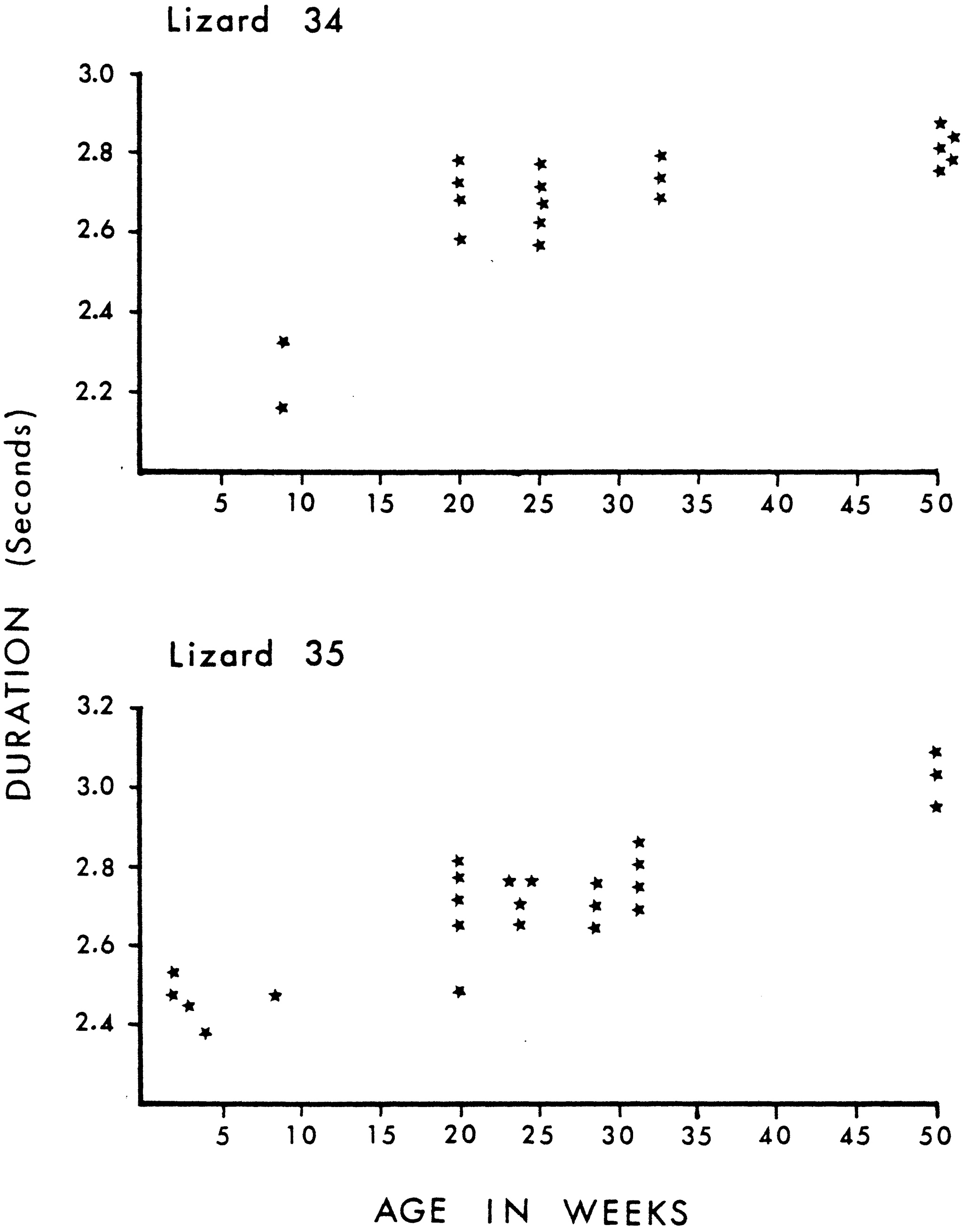
Fig. 9. For both A and B Displays, the means and 95% confidence intervals of Core Duration and Post-Core Duration at Agegroups 1, 2, and 3. These are the means of the individual lizard means.

Appendix I. Number of displays recorded from each lizard at each Weekgroup. Sex of individuals is indicated where known.

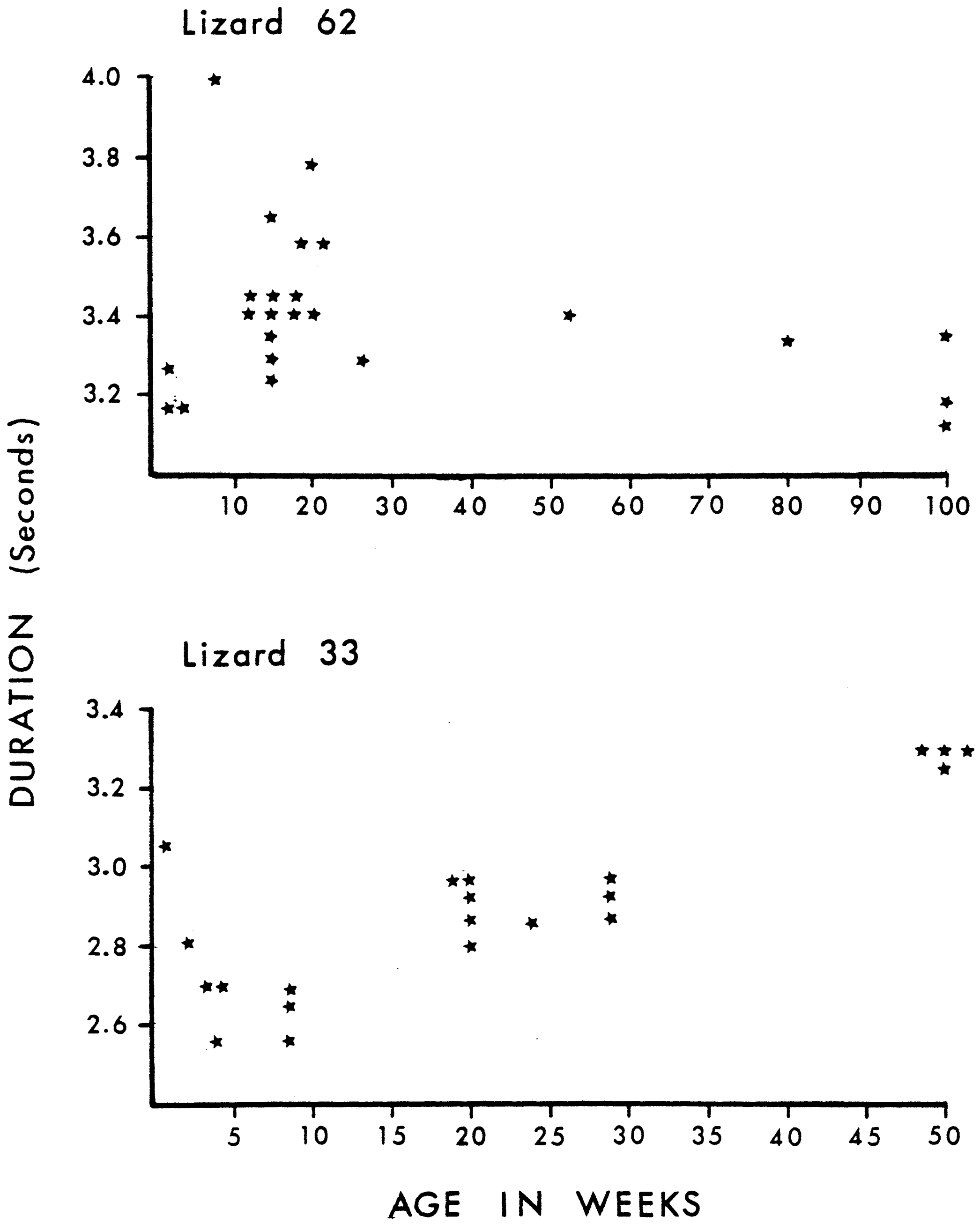
| Lizard | Sex | Weekgroup | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 0.5 | 1 | 2 | 4 | 8 | 20 | 28 | 52 | 100 | T |
| 17 | F | 10 | 6 | - | 3 | 1 | - | - | - | - | 20 |
| 18 | F | 1 | 1 | 1 | 3 | - | - | - | - | - | 6 |
| 20 | M | 7 | 8 | 4 | 6 | 1 | - | - | - | - | 26 |
| 24 | F | - | - | 2 | 2 | 3 | 1 | 8 | - | - | 16 |
| 25 | F | 2 | 2 | 2 | 6 | - | - | - | - | 10 | 22 |
| 26 | M | 2 | - | - | - | 4 | - | - | - | 13 | 19 |
| 27 | M | - | - | 3 | 1 | 6 | 4 | 5 | - | 10 | 29 |
| 31 | M | - | - | - | - | - | - | 5 | 11 | 19 | 35 |
| 32 | F | 2 | - | 2 | 2 | - | 4 | 4 | 6 | - | 20 |
| 33 | M | 2 | 3 | 6 | 3 | 5 | 6 | 13 | 7 | - | 45 |
| 34 | M | 5 | - | - | - | 2 | 11 | 8 | 23 | - | 49 |
| 35 | M | 12 | 6 | 8 | 5 | 7 | 8 | 27 | 20 | - | 93 |
| 36 | M | 3 | - | 2 | 1 | 1 | 4 | 9 | 7 | - | 27 |
| 37 | F | 3 | - | 4 | 1 | 4 | 10 | - | 10 | - | 32 |
| 38 | F | 5 | - | 5 | 3 | 2 | 4 | 4 | 8 | - | 31 |
| 39 | F | 1 | - | - | 1 | 1 | 6 | 4 | - | - | 13 |
| 40 | M | 2 | - | - | 3 | - | 2 | - | 8 | - | 15 |
| 50 | F | 1 | - | 2 | - | 5 | 1 | - | 1 | - | 10 |
| 51 | F | - | - | - | - | - | - | - | 1 | 12 | 13 |
| 52 | F | 1 | - | - | - | 2 | 4 | - | 2 | - | 9 |
| 54 | M | 6 | 6 | 5 | 5 | 6 | 8 | 3 | - | - | 39 |
| 58 | M | - | 10 | 6 | 8 | 5 | 16 | 8 | - | - | 53 |
| 62 | M | 1 | - | 4 | 2 | 1 | 39 | 4 | 2 | 8 | 61 |
| 74 | M | 1 | 8 | 2 | - | 7 | - | - | - | - | 17 |
| 76 | | 5 | 1 | 1 | - | - | - | - | - | - | 7 |
| 77 | | 45 | 3 | 6 | 3 | - | - | - | - | - | 57 |
| 78 | | 7 | 1 | 17 | 2 | - | - | - | - | - | 27 |
| 79 | | 9 | 1 | 4 | 4 | - | - | - | - | - | 18 |
| 80 | | 2 | 1 | 1 | 8 | - | - | - | - | - | 12 |
| 85 | | 2 | - | 1 | 14 | - | - | - | - | - | 17 |
| 87 | | 9 | 2 | 3 | 3 | - | - | - | - | - | 17 |
| 88 | | 30 | - | 1 | 1 | - | - | - | - | - | 32 |
| 89 | | 3 | 1 | 5 | 1 | - | - | - | - | - | 10 |
| 92 | M | - | - | 2 | - | - | 6 | - | - | - | 8 |
| 93 | F | - | 4 | 2 | 8 | 3 | 3 | 1 | - | - | 21 |
| 94 | F | - | 3 | 1 | 1 | 3 | 4 | 5 | - | - | 17 |
| T | | 184 | 61 | 100 | 107 | 62 | 146 | 114 | 114 | 53 | 943 |



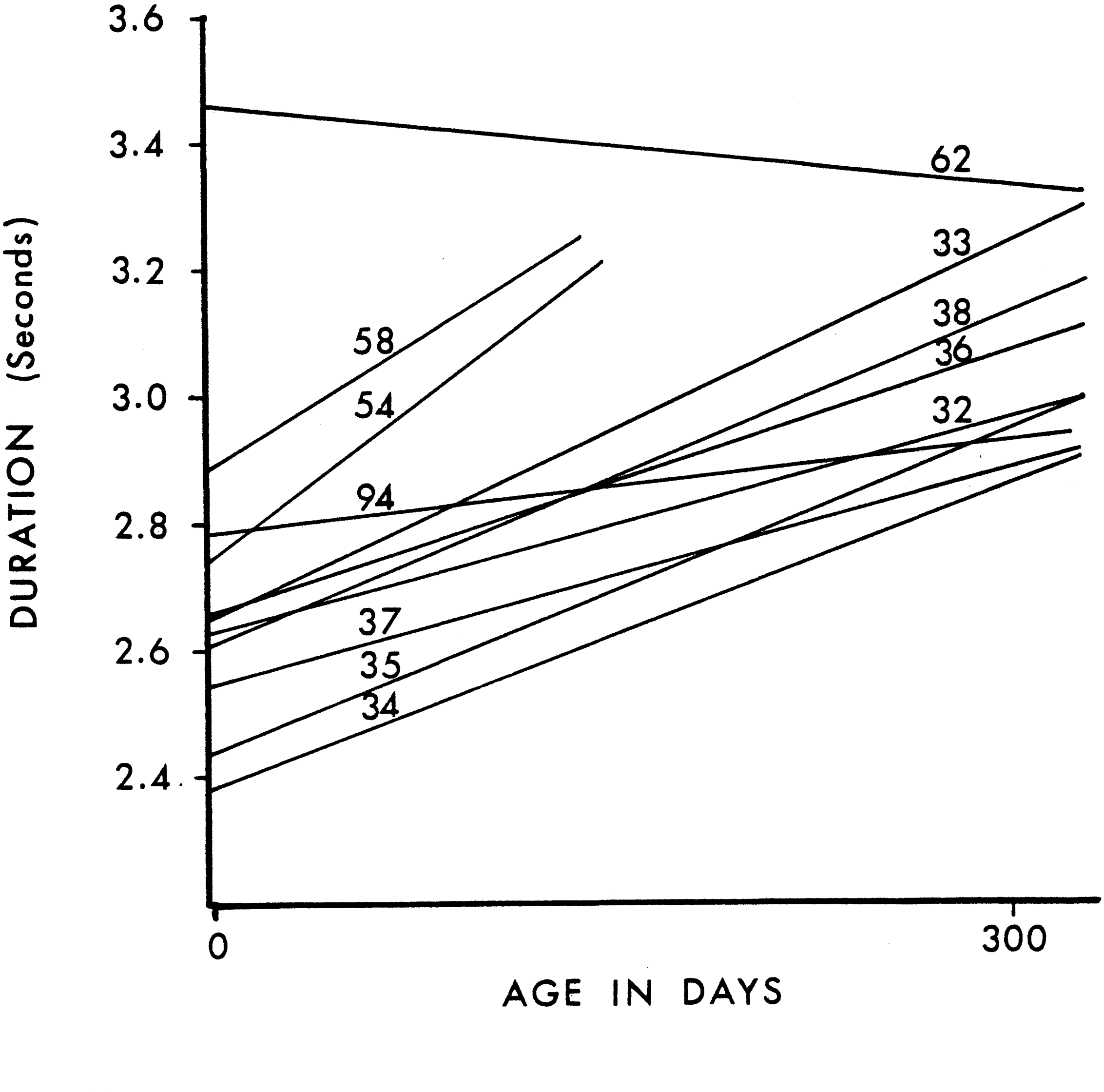
Appendix II. Plots of the Core Duration of A Displays for six lizards. Each star represents one observation. Plots of individual unit durations for both A and B Displays appear very similar to these. Continued on the following two pages.



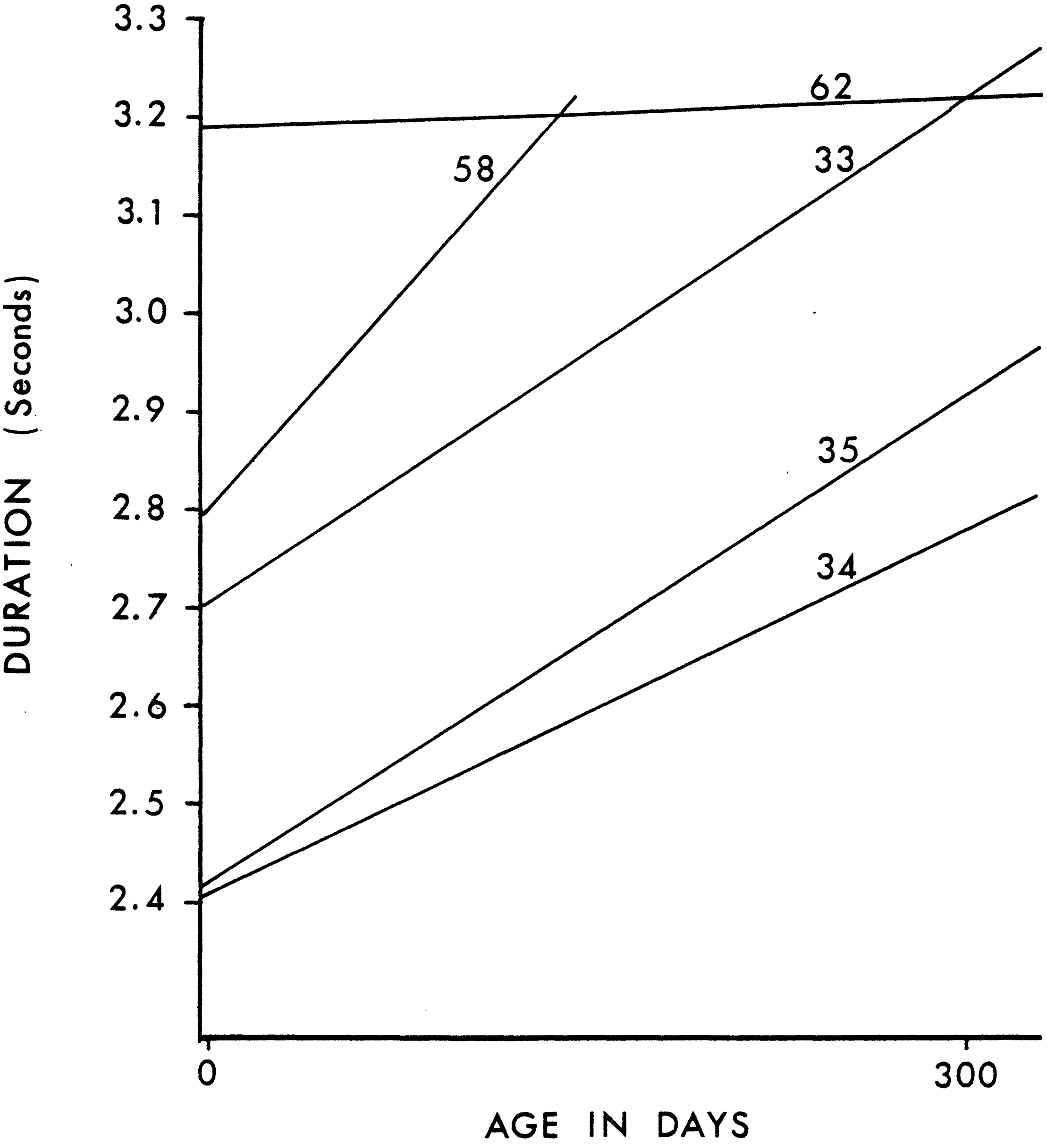
Appendix II, continued.



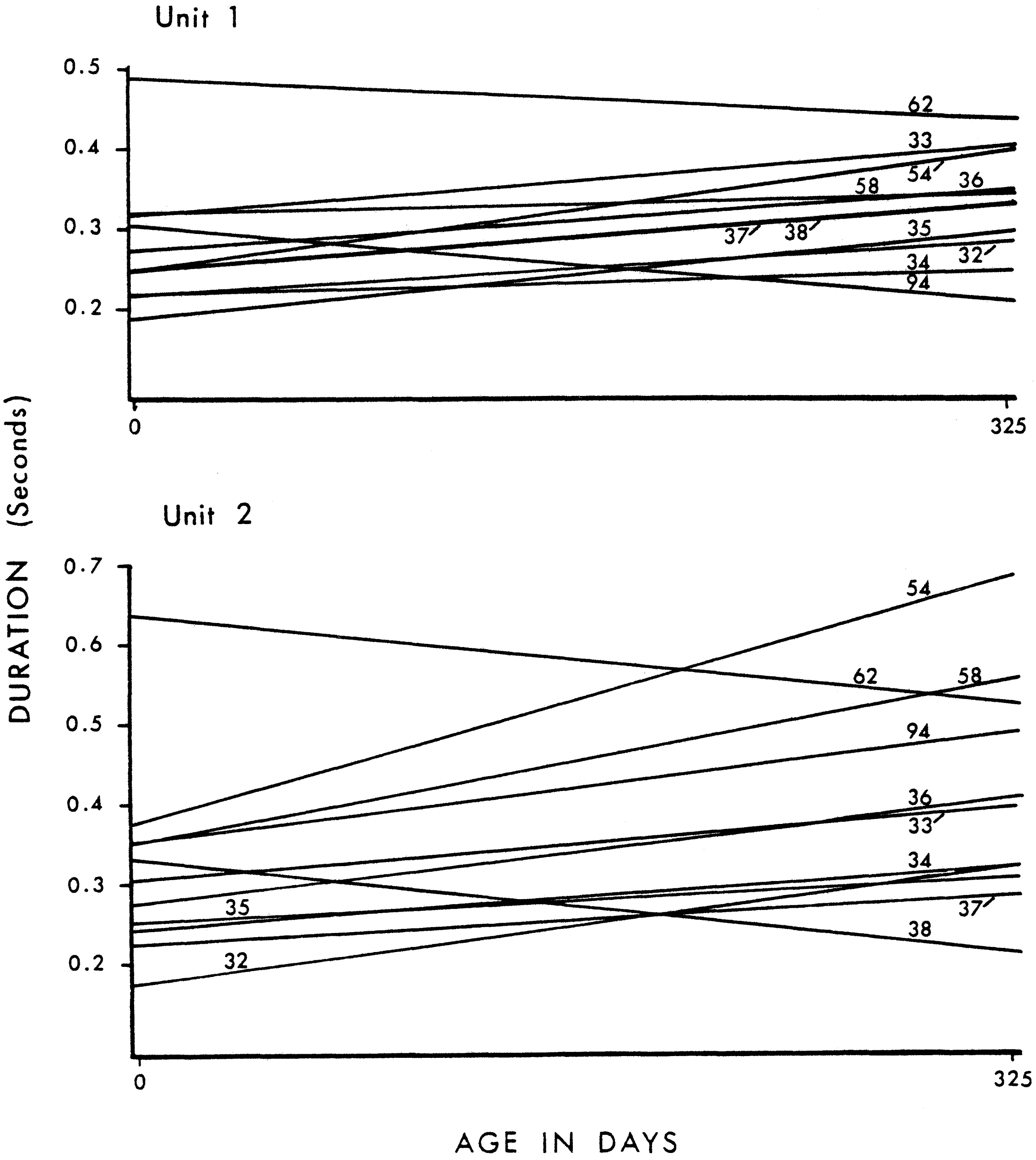
Appendix II, continued.



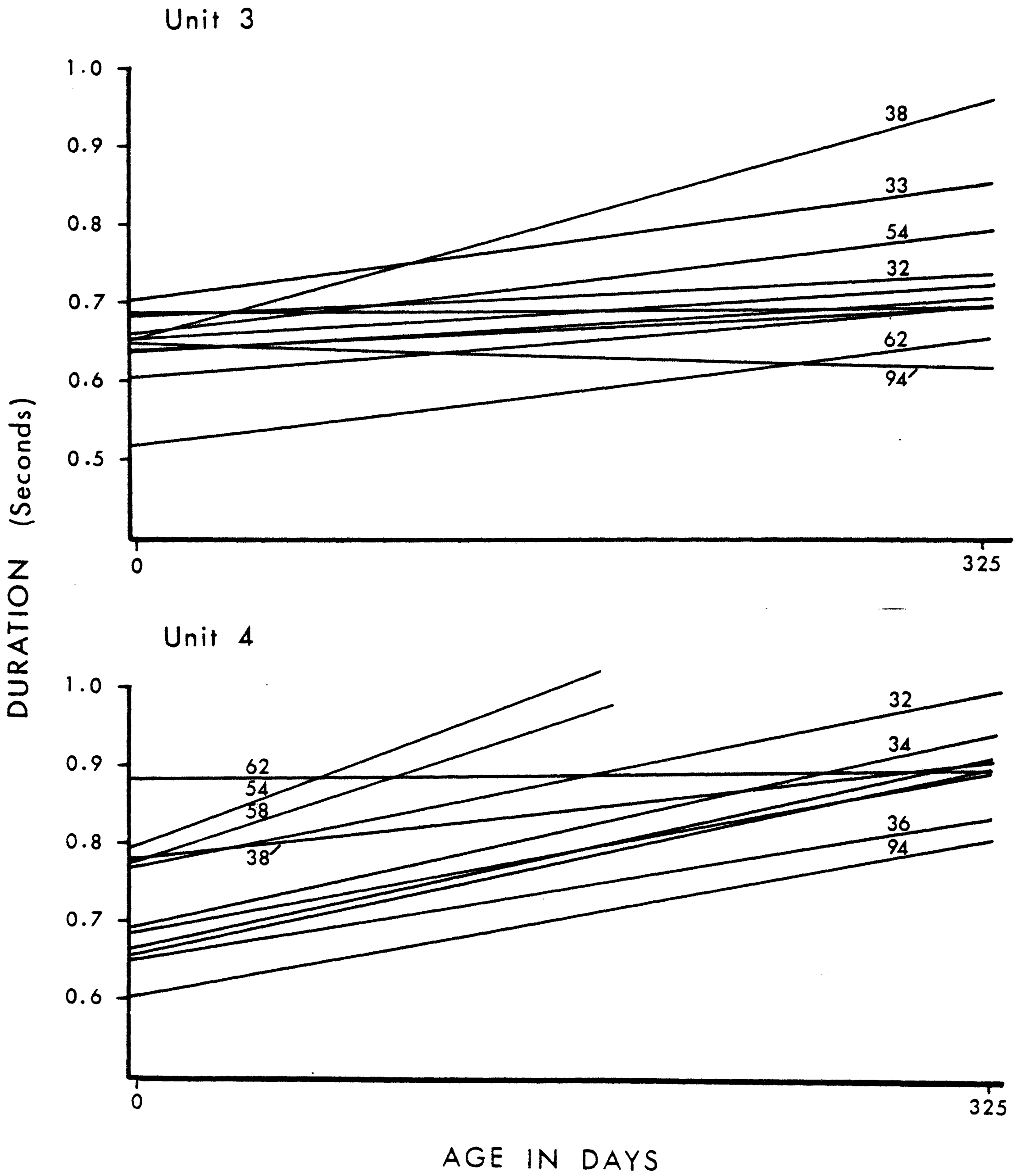
Appendix III. Plots of the regression lines of Core Duration against Age in Days for A Displays (this page) and for B Displays (following page). Each line represents one individual, identified by number; numbers with the same first digit belong to lizards from the same clutch.



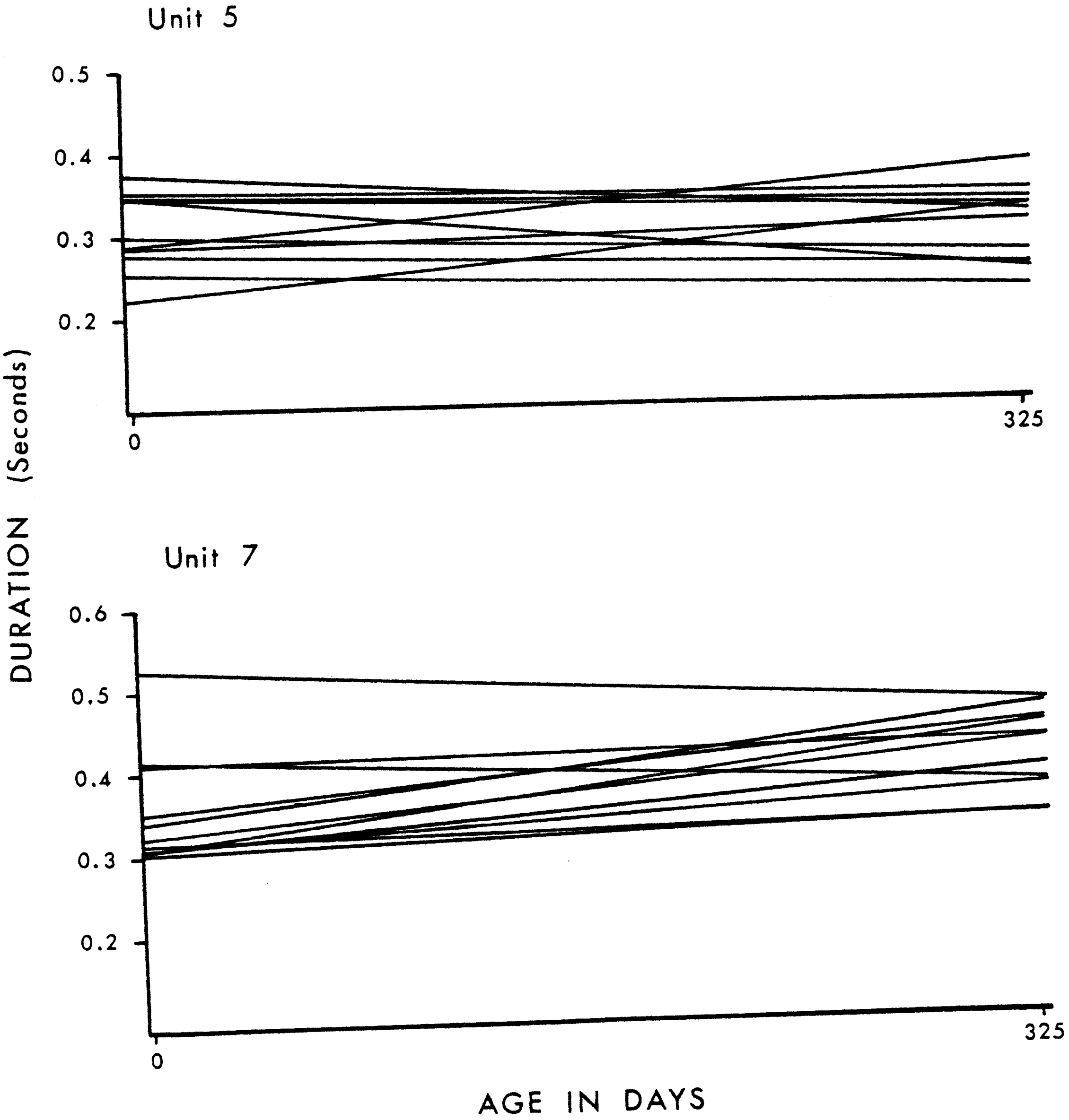
Appendix III, continued.



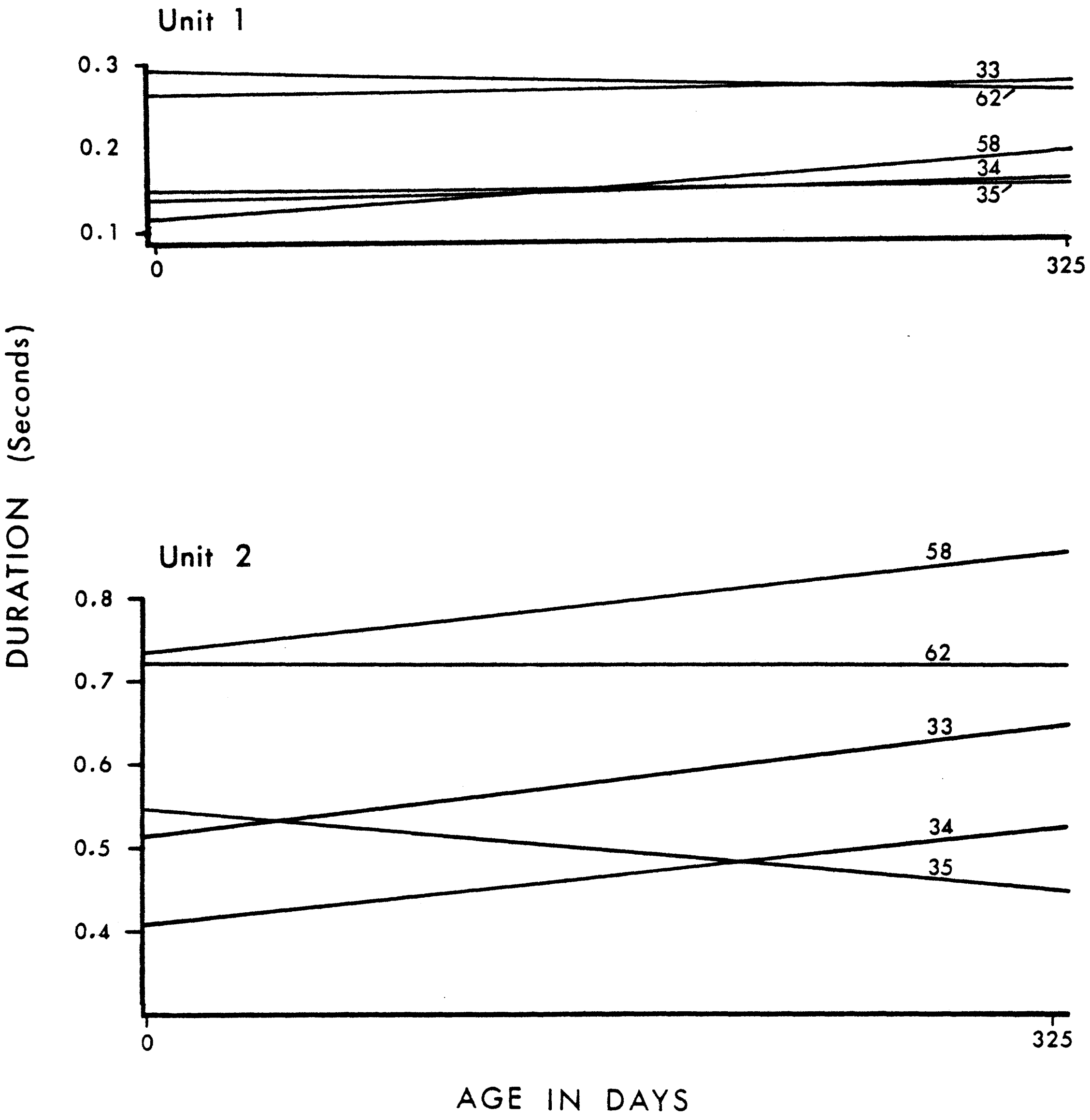
Appendix IV. For A Displays, plots of the regression lines for durations of Units 1-7 against Age in Days, for 11 lizards. Lines for each lizard are identified by number in most cases; numbers with the same first digit belong to lizards from the same clutch. Continued on the following two pages.



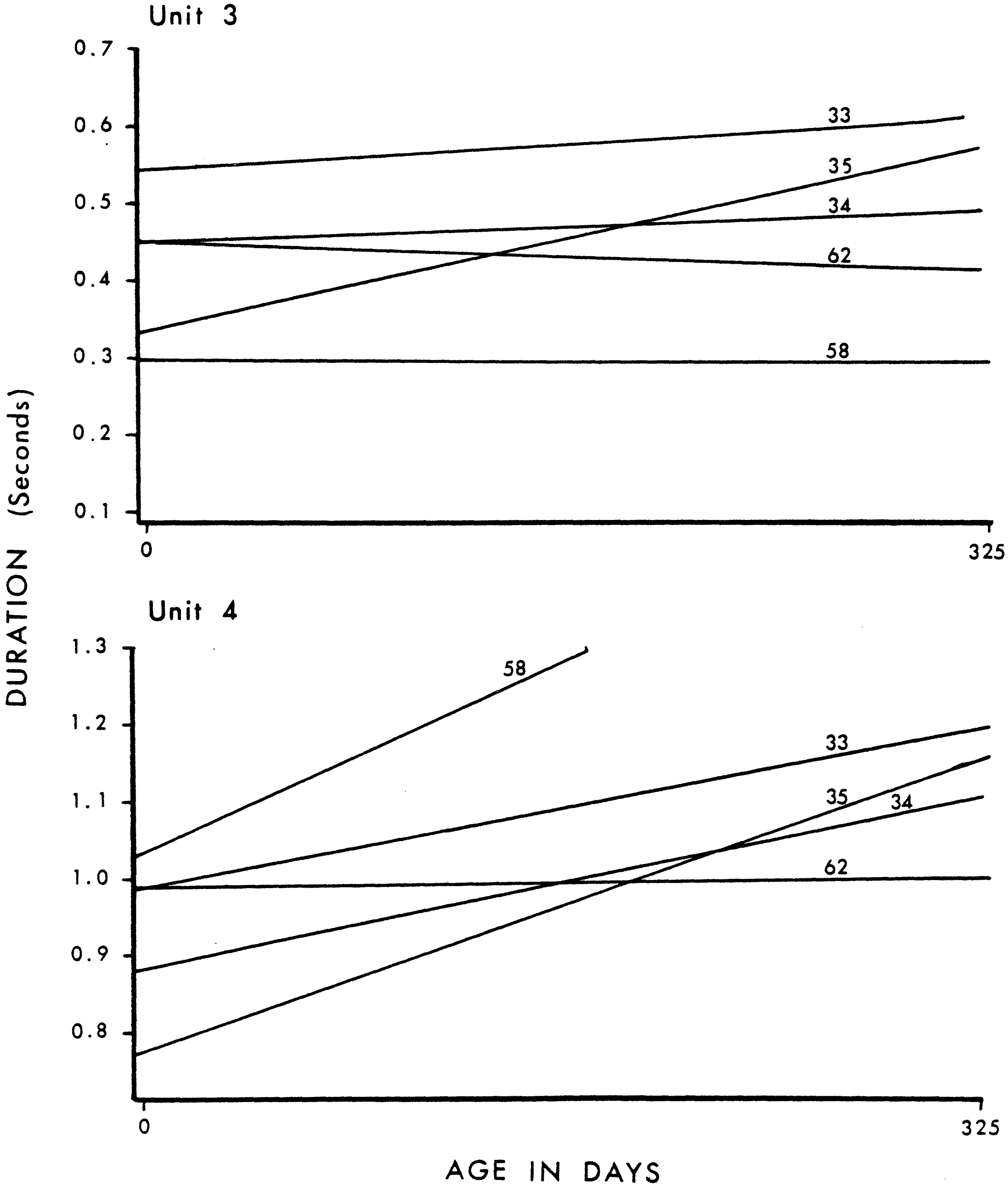
Appendix IV, continued.



Appendix IV, continued.



Appendix V. For B Displays, plots of the regression lines for durations of Units 1-7 against Age in Days, for 5 lizards. Lines for each lizard are identified by number in most cases; numbers with the same first digit belong to lizards from the same clutch. Continued on the following two pages.



Appendix V, continued.

Appendix V, continued.

## Appendix VI. Percentage of Variance in Units 1-12 due to Clutch, Lizards within Clutch, Weekgroup, and Error.

| | Units | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| A Displays | | | | | | | | | | | | |
| Clutch | 39 | 55 | 28 | 13 | 13 | 30 | 15 | 30 | 38 | 28 | 45 | 27 |
| Lizards | 24 | 24 | 28 | 38 | 40 | 12 | 49 | 19 | 2 | 15 | 15 | 25 |
| Weekgroup | 8 | 8 | 11 | 26 | 1 | 5 | 6 | 4 | 0 | 3 | 2 | 8 |
| Error | 29 | 14 | 33 | 22 | 46 | 53 | 29 | 46 | 60 | 61 | 39 | 40 |
| B Displays | | | | | | | | | | | | |
| Clutch | 24 | 61 | 47 | 0 | 1 | 17 | 0 | 38 | 0 | 25 | 0 | 13 |
| Lizards | 36 | 8 | 28 | 50 | 42 | 33 | 34 | 22 | 74 | 42 | 23 | 0 |
| Weekgroup | 5 | 3 | 4 | 14 | 0 | 5 | 2 | 6 | 0 | 10 | 8 | 9 |
| Error | 35 | 27 | 21 | 37 | 57 | 45 | 64 | 34 | 26 | 24 | 69 | 78 |

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# ONTOGENY OF DISPLAY BEHAVIOR IN
# SCELOPORUS UNDULATUS HYACINTHINUS
# (SAURIA: IGUANIDAE)

By

Madeleine E. Roggenbuck

## (ABSTRACT)

Displays of 36 Sceloporus undulatus hyacinthinus from 8 clutches were recorded on video tape from the day of hatching to adult size during 1978, 1979, and 1980. Nine hundred forty-one displays were analyzed frame by frame, and durations of display units were calculated to the nearest 0.01 s.

From the day of hatching, males and females performed both of the display types found in adults, and little significant ontogenic change was found in display patterns or in unit durations; only 7% and 6% of total variance in A and B Displays, respectively, was due to ontogeny. Stereotypy of unit durations both within and among lizards was unchanged across time. Consequently, the display patterns are viewed as being purely innate.

Some ontogenic changes were observed in the ways in which the lizards utilized the displays patterns. As compared with hatchlings, older lizards tended to display more frequently, to use display modifiers more often, and to

perform displays in aggressive and courtship contexts as well as in assertion. Older females had a significantly higher A:B ratio than males or younger females. These changes in display behavior are viewed as being due to the influences of hormones and social experiences.

Slightly more than half of the variance in unit durations for A and B Displays was attributed to inter-individual differences. Of this, approximately half was due to differences among clutches and half to differences among lizards within clutches. For B Displays there were some inter-individual differences (e. g., deleted bobs or dips preceding certain bobs) in the form of the displays as well as in unit durations. Individuals were not consistent in the inclusion of these characteristics in their B Displays.

Mean heritability estimates for durations of units 1-12 were 0.60 and 0.38 for A and B Displays, respectively.