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The Ontogeny of Display Behaviour in *Sceloporus undulatus* (Sauria: Iguanidae)

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With 6 figures

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Abstract

A longitudinal study (from neonate to adult) was made of the display behaviour of 36 fence lizards from 8 clutches. A frame-by-frame analysis of 941 video-taped displays revealed that the hatchlings possessed almost all of their adult display patterns by the first two days of life. Of the total variance in the display behaviour, 7 % or less was attributed to experience. Of the variance among lizards, approximately half came from between clutches and half from between clutchmates. Our data indicate that the visual communication signals (head bob displays) of this vertebrate species are almost totally innate.

Introduction

The head-bobbing displays of agamid and iguanid lizards serve as social signals for territorial defense and courtship (CARPENTER 1967; JENSSEN 1977). They are an excellent example of a modal action pattern (sensu BARLOW 1977) in vertebrates, and have long been assumed to be an innate and species-specific class of behaviours (CARPENTER 1967: 102). Yet little is known about the ontogeny of the display patterns, or how resistant they may be to the influence of experience (BURGHARDT 1978; HAILMAN 1977: 311). There are only anecdotal observations on the displays of hatchlings (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 published longitudinal data on the early development of display behaviour for any saurian species.

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The present investigation is a laboratory study of the development of display behaviour by the fence lizard, *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 display over time; and (3) to compare features of the displays both within and between clutches as a means of evaluating genetic influences on display behaviour.

Background

Rothblum & Jenssen (1978) described the display behaviour of adult male *S. u. hyacinthinus,* and their study serves as a base of comparison for our research. They found two similar, but statistically distinct display patterns, designated Type A and Type B (Figs. 1, 2). These displays 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 bobs and shorter interbob pauses 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, which was less than 1.0 for A Displays and greater than 1.0 for B Displays (Rothblum & Jenssen 1978). Another difference between the display types was in the relative amplitudes of

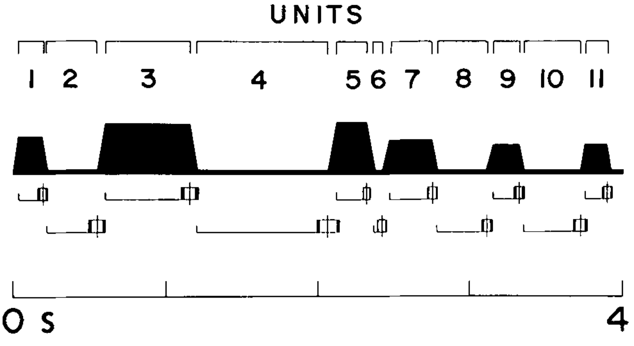

Fig. 1: The average Type A Display of adult male *Sceloporus undulatus hyacinthinus.* The display has been divided into units, with unit duration given by a horizontal line, mean duration by a vertical line, and 95% and 99% confidence intervals by the outer edges of the white and black bars (after Rothblum & Jenssen 1978)

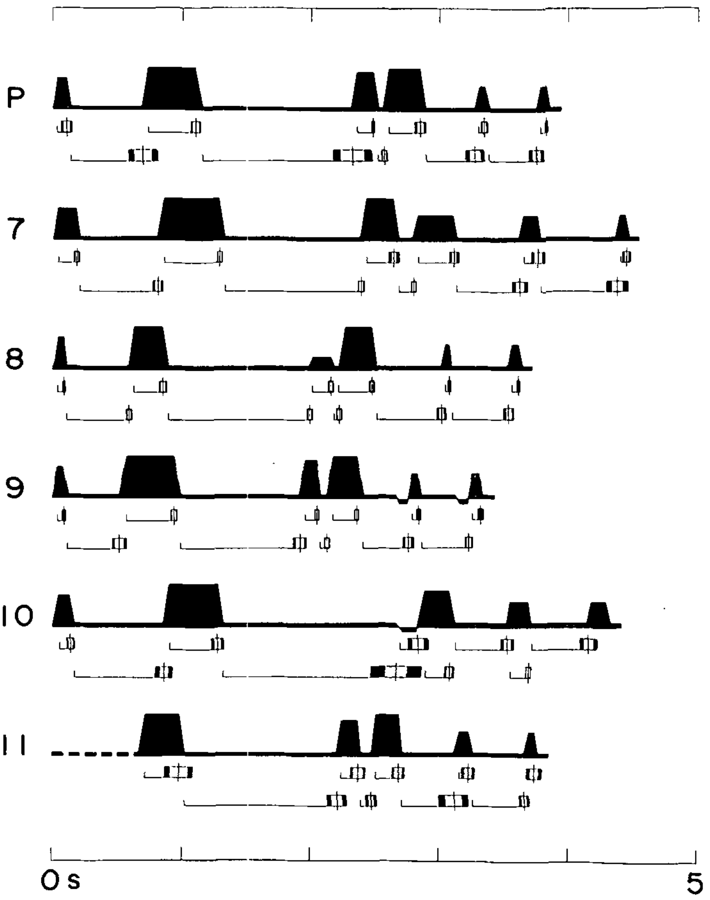

Fig. 2: The average Type B Display (P) pooled from 6 adult male *Sceloporus undulatus hyacinthinus* having a common pattern, and five Type B patterns for individual males (7—11) having individually unique Type B patterns (after ROTHBLUM & JENSSEN 1978)

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.

Type A Displays were stereotyped both within and among adult lizards; in contrast, more than half of the lizards 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 (ROTHBLUM & JENSSEN 1978; Fig. 2). Therefore, no single Type B pattern was characteristic of the population. This apparent combination of a stereotyped behaviour at the population level (Type A Display) and of patterns that are distinct among lizards at the population level (Type B Display) provided a promising opportunity to examine ontogeny in a vertebrate communication system.

Materials and Methods

Subjects and Maintenance

The fence lizard has a wide distribution in the United States, where it is represented by six geographic forms (TINKLE & BALLINGER 1972). We studied *S. u. hyacinthinus*, the only sceloporine north of Georgia and east of Texas (CONANT 1975). This lizard is relatively small (max. snout-vent length = 83 mm), gray or brown in colour, largely arboreal, and an inhabitant of woodland edges.

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 & 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 %.

Hatchlings were toe-clipped for individual identification, and sexed by the size of the post-anal scales. Hatchlings were maintained in groups of 1—10 in a variety of cages ranging from 38 to 151 l in size. Each cage was provided with stumps, sticks, soil, and bark litter. A natural (seasonal) photoperiod was supplemented with both fluorescent Vitalites 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.

Display Analysis

Using the videotape equipment and techniques of ROTHBLUM & JENSSEN (1978), 554 A and 389 B displays by 36 lizards (17 females and 19 males) from 8 clutches were recorded and analyzed. A mean of 26 displays (SE ± 3.1) per lizard was recorded, with the last display videotaped on the average 266 days (SE ± 5.7) after hatching. For 75 % of the subjects, taping began on the first day of hatching, with an effort made to record displaying lizards daily during the first week of life, weekly during the

Table 1: Variables used in the data analyses of each display

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) Key ratio	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
25) Bob 4 dip	Presence or absence of dip preceding Bob 4
26) End dips	Presence or absence of dips preceding terminal bobs

following month, and approximately monthly thereafter. During taping sessions, an increase in display frequency was occasionally obtained by placing the subjects into a novel cage, exposing them to a new cagemate, or providing them with food.

96 variables were recorded for each recorded display (Table 1). Most of these variables were derived from a frame-by-frame temporal analysis of the head bob display. In this analysis, vertical changes in the lizard's head amplitude were measured throughout the display's duration at 0.01 s increments to precisely delineate each bob and interbob pause and quantify their respective durations (see ROTHBLUM & JENSSEN 1978). As shown in Fig. 1, each bob and interbob pause was designated as a unit. The first 12 units of each display were used in our analysis.

Table 2: Three time classifications of displays. Age (in days) is the age of the lizard at the time the display was performed. The numerical labels of the Weekgroup categories refer to the age in weeks of the oldest possible displayer for a Weekgroup class

Age (in days)	Weekgroup	Agegroup
0 — 3	0.5	
4 — 7	1	1
8 — 14	2	
15 — 18	4	
29 — 56	8	2
57 — 140	20	
141 — 196	28	
197 — 365	52	3
> 366	100	

Type A and B Displays were segregated according to the criteria of ROTHBLUM & JENSSEN (1978) as reviewed above. As a check that the A and B Displays of our study were correctly labeled, a discriminant function analysis (JENRICH & SAMPSON 1977) was performed on all displays, including the very first to appear when display anomalies were more likely to occur. The analysis was based on the duration of each of the units 1—9, and on the variables, Ratio and Key ratio (see Table 1). The analysis agreed with our designations in 99.4 % of the A Displays and 97.1 % of the B Displays (Fig. 3). The three most important variables for making the discrimination were the duration of Units 3, 4, and 9.

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,

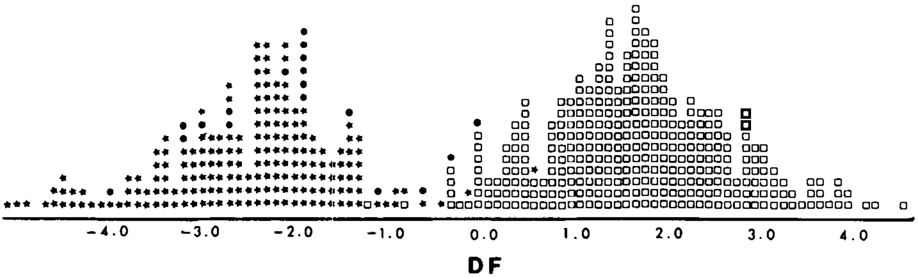

Fig. 3: The distribution of Type A (squares) and Type B (stars) Displays of *Sceloporus undulatus hyacinthinus* as apportioned by discriminant function analysis (variables used are listed in text)

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, type I (BARR et al. 1979) estimated 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 two 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 7 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.

While most juvenile displays had the same patterns reported for adult males (Figs. 1 and 2), the very earliest displays often consisted of only two or three bobs and differed from subsequent displays by having bobs with much lower amplitudes. 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.

Early displays commonly exhibited two other features atypical of adult displays. Of the displays in Weekgroup 0.5, 68 % had bobs that were "rounded" rather than plateaued; that is, the lizard's head ascended and descended slowly rather than abruptly (Table 3). In 49 % of the displays performed within Weekgroup 0.5, the third and fourth bobs were given as a single bob or as a single bob that was "stepped" (Fig. 4 and Table 3).

Ontogenic Changes from Hatching to Maturity

Changes in Total Bobs. There was a progressive increase between the three Agegroups in the mean number of bobs per display: 5.3 → 7.0 → 7.4 for A Displays and 5.3 → 7.2 → 8.5 for B Displays. For both A and B Displays, this increase was significant between Agegroups 1 and 2 ($p < 0.001$, Mann Whitney U test).

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. Numbers in parenthesis represent sample sizes

Weekgroup	A	B	C
0.5	68 (125)	49 (90)	10 (18)
1	49 (30)	16 (10)	11 (7)
2	36 (36)	16 (16)	13 (13)
4	31 (33)	11 (12)	9 (10)
8	10 (6)	18 (11)	5 (3)
20	11 (16)	9 (13)	11 (16)
28	4 (5)	5 (6)	2 (2)
52 (1 year old)	10 (11)	0 (0)	4 (5)

Changes in Ratio of A : B Displays. Both male and female lizards tended to perform more A than B Displays. 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 (N = 460). Females tended to have higher A : B display ratios than males, being 1.9 for Agegroup 1 (N = 80), 1.6 for Agegroup 2 (N = 114), and 3.3 for Agegroup 3 (N = 77). Only females of Agegroup 3 had a significantly different ratio from any of the other male or female Agegroup classes (χ^2 test, $p < 0.05$). Thus, females approaching adulthood performed fewer B displays than any other age and sex class of lizards. Although the difference in message content between A and B Displays is not known, it is possible that the B Display indicates a higher level of agonistic intent than does the A Display (ROTHBLUM & JENSSEN 1978).

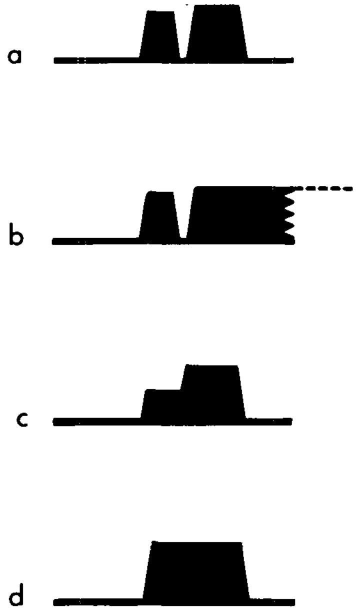

Fig. 4: Four forms of bobs 3 and 4 that were observed at times in both Type A and Type B Displays of *Sceloporus undulatus hyacinthinus.* (a) Complete separation of the bobs in the normal pattern; (b) failure of head to descend from bob 4; (c) a single "stepped" or shouldered bob, without 2 distinct bobs; and (d) only a single, long bob rather than two shorter bobs

A : B ratios for individual lizards varied considerably. Ratios for individual males ranged from 0.53 (9 A : 17 B) to 4.00 (28 A : 7 B), and those for females ranged from 0.83 (25 A : 30 B) to 9.00 (18 A : 2 B).

Changes in Unit Durations. Many bob and pause durations increased or decreased slightly during the study period; however, changes were not observed for all lizards nor for all units, and few of the observed changes were significant. For those individual lizards ($N = 11$) having the largest sample sizes of displays ($\overline{X} = 48$, range 31—93), we computed linear regressions of unit durations against age in days; 62 % of these regressions for A Display units, and 76 % of the regressions for B Displays units, did not significantly deviate from a zero slope ($p > 0.05$; ROGGENBUCK 1982). However, Unit 4 significantly lengthened with age in 10 of the 11 lizards for A Displays, and in 4 of the 5 lizards for B Displays; Core Duration also lengthened significantly for most lizards.

Of the total variance in unit durations only 7 % and 6 % for A and B Displays, respectively, could be attributed to changes through time. In contrast, 54 % and 51 % of the total variance in A and B Displays, respectively, was attributed to differences among individuals. Of this, approximately half was attributed to differences among clutches, and half to differences among individuals within clutches (variance components analysis, Table 4).

Changes in Stereotypy of Unit Durations. We had speculated that unit variance for the displays would decrease with age: (1) for a given juvenile (increasing intra-individual stereotypy); and (2) for the population of juveniles

Table 4: Variance components analyses showing the percentage of total variance in the durations of Units 1—12 (averaged), and in Core Duration, 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) error (largely with individuals)

	Dependent variables	
	Units 1—12 (mean ± SD)	Core duration
Independent variables		
A Displays		
Total among lizards component	54	69
(among clutches)	30 ± 13	40
(among lizards within clutches)	24 ± 13	29
Among Weekgroups	7 ± 7	20
Error	39 ± 15	11
Total	100	100
B Displays		
Total among lizards component	51	49
(among clutches)	19 ± 21	0
(among lizards within clutches)	32 ± 19	49
Weekgroup	6 ± 4	25
Error	43 ± 20	24
Total	100	100

(increasing inter-individual stereotypy), with the population converging on the adult pattern. These speculations were not supported as the following analysis and results show.

Intra-individual stereotypy was assessed by calculating the coefficient of variation (C. V. = S. D. × 100/mean) for Units 1—7 of each lizard's displays. These within-lizard C. V.'s were then averaged across lizards to obtain a mean C. V. value for each unit, and then averaged across the 7 units to obtain a single, average coefficient of variation representing intra-individual stereotypy. This was done separately for each of the three Agegroups, yielding values of 15 %, 19 %, and 14 % at Agegroups 1, 2, and 3, respectively, for A Displays; and 25 %, 19 %, and 15 % for Agegroups 1, 2, and 3, respectively, for B Displays.

Inter-individual stereotypy was assessed by first averaging the durations of Units 1—7 for each lizard. Thus with 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. These 7 C. V. values, one for each of Units 1—7, were averaged to obtain a single value representing inter-individual stereotypy. This was done separately for each of the three Agegroups, yielding values of 24 %, 25 %, and 23 % at Agegroups 1, 2, and 3, respectively, for A Displays; and 27 %, 24 %, and 27 % at Agegroups 1, 2, and 3, respectively, for B Displays.

Inspection of the narrow breadth of the 95 % confidence intervals for unit durations (Figs. 5 and 6) also reveals that there was no tendency for older Agegroups to have less variance; contrary to our expectation, there was no evidence that the displays of the juvenile population get more stereotyped and converge on a common adult pattern with age; the stereotyped patterns exist from the start, with little change through time.

Sex Differences in Unit Durations

For both A and B Displays, males and females did not differ significantly in their average unit durations, Core Duration, and Total Bobs.

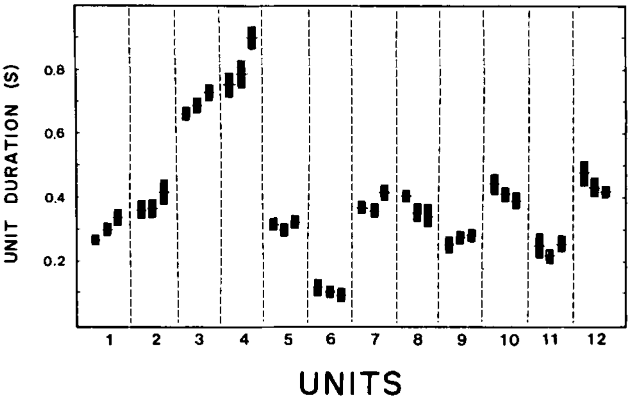

Fig. 5: Descriptive statistics for unit durations of *Sceloporus undulatus hyacinthinus* Type A Displays. Horizontal lines indicate the average of each lizard's mean unit duration, and vertical bars denote their 95 % confidence intervals. For each unit, data are arranged left to right for age groups 1—3

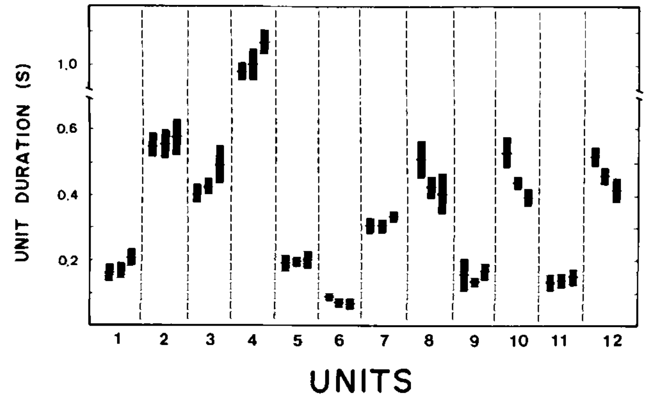

Fig. 6: Descriptive statistics for unit duration of *Sceloporus undulatus hyacinthinus* Type B Displays. See Fig. 4 legend for additional notation

Individual Differences in Display Patterns

Because the pattern deviations of B Displays had appeared to be individually unique for adult males (ROTHBLUM & JENSSEN 1978), we hypothesized that the deviant B Display patterns might be genetically set and that clutch mates might have more similar variants of the B pattern than lizards from different clutches. Our data, however, marginally supported this hypothesis at best.

We found the same B pattern variations as described by ROTHBLUM & JENSSEN (1978, Fig. 2) for adult lizards; these were, for example, deleted Bob 1 or Bob 3, a dip preceding the fourth bob, and dips preceding the terminal bobs (End Dips). However, individuals were not always consistent in their B Display patterns (ROGGENBUCK 1982). At times the juveniles performed one of the deviant B patterns, but then the same individuals would also give the normal B Display.

Nevertheless, lizards from different clutches tended to share the same range of B pattern deviations. For example, lizards in 6 of the 8 clutches featured a dip before Bob 4 in some of their B Displays; among these clutches the percentage of all B Displays featuring this dip ranged from 12 % to 78 %. 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.

Dual-Environment Comparisons

As a test of the relative influence of genetic control upon the display behaviour of *S. u. hyacinthinus,* we compared the displays of lizards with similar genetic composition but exposed to different rearing conditions. One group of lizards (present study) was removed from the field while *in utero* and performed their displays while living in the confined conditions of the laboratory. The second group consisted of wild-caught adult males (ROTHBLUM & JENSSEN 1978) from the same deme. Unit durations for the A Displays in the two groups were almost identical, showing only a 5.2 % difference on the average, despite the many experiential factors which differed between the groups.

Discussion

Many current ontogenic issues revolve around the nature of the limits set by different genotypes on phenotypes (BATESON & KLOPFER 1982; BURGHARDT 1977). A present challenge is to evaluate those limits for a given behaviour and compare them with the limits of similar behaviour of other species. When comparing communication signals across taxa, one finds a phylogenetic continuum with regard to degree of correspondence between genotype and phenotype. At one end of this spectrum are signals with little potential for modifiability, such as cricket stridulations (OTTE 1977); at the other end are human vocalizations, which are much more affected by experience (GOULD 1982). Along this continuum, the head bob displays of *Sceloporus undulatus* fall close to the cricket call model; hatchlings just a few h old performed adult-like displays which appear autogenous, with little influence from extrinsic factors.

Of the factors which BURGHARDT (1977) listed as potential modifiers or precursors of communication behaviour (e. g., genotype, maturation, hormones, sensitive periods, habituation, reinforcement, association, and insight), only genotype is a major factor shaping *S. undulatus* display patterns. Both the A and B patterns were differentiated from the day of hatching; the rapid appearance of the closely timed sequence of bobs, in some cases observed in lizards less than an h old, speaks against a priming or releasing hormonal agent. Furthermore, because there is no parental care in this precocial species, the lizard neonates have no opportunity to modify their signals through imprinting or associative learning from parents. Any kind of longitudinal learning effect was very weak at best, because only 6—7 % of total variance in unit durations was attributed to increasing age. Thus, this communication behaviour reflects very narrow genotypic limits on the phenotype.

There may exist, however, a more fascinating ontogenic effect on lizard signals than that involving the displays' physical characteristics. Our study has established that the bob patterns of *S. undulatus* are fixed within several days of hatching, with little variance in a lizard's displays through time. Therefore, the physical form of these social signals seems little affected by ontogenic change. However, the development of the function of these signals may actually reflect a much more dramatic ontogenic influence. Consider that the head bobbing of a lizard is a visual signal that is encoded with a message (sensu SMITH 1969, 1977), and this message represents some "intent" on the part of the signaler (BURGHARDT 1970). The signal is decoded by a recipient to produce a meaning which may result in the recipient responding in a manner concordant with the signaler's intent. This "message-meaning" or "intent-response" relationship of a signal undoubtedly has a developmental phase which, in a lizard, may last its entire life. From hatching, the lizards are genetically endowed with their head bob displays, but there is evidence that hatchlings may not use and respond to the displays in as specific a context and manner as do adults.

Although our study was not set up to analyse the contexts in which displays appeared and the response to the displays, hundreds of hours of observations and of viewing videotapes did result in numerous anecdotes and in some general impressions. The most striking impression was the absence of any clear context for the displays of hatchlings. Social interactions of hatchlings, unlike those of adults, did not clearly reflect dominance or territoriality, and hatchlings had a tendency to be gregarious which seemed to transcend the space limitations of their cages. Although hatchlings displayed frequently, the use of display modifiers (which in adults indicate increasing levels of aggression, see ORTIZ & JENSSEN 1982) was rare, as were chasing, biting, and prolonged bouts of displays. In short, displays of hatchlings did not appear to be performed in an aggressive manner as STAMPS (1978) observed with juvenile *Anolis aeneus*. Some of the situations in which displays were performed suggested play, involving voluntary, irrelevant behaviour in inappropriate contexts. Two of the six categories of play activities presented by MCFARLAND (1982), practice behaviour and social play, seemed to fit, at least superficially, the observed hatchling behaviour (ROGGENBUCK 1982).

At what points during ontogeny do the neonates gain the adult message-meaning (e.g., territorial advertisement, aggression, courtship) associated with the physical signals? A longitudinal study which correlates context with display usage and recipient response is the next step to investigate this intriguing ontogenic question. It is likely that at this level of analysis we will find that such experiential factors as hormonal agents, conditioned learning, and perhaps play (but see BURGHARDT 1984) will have significant effects upon the function of reptilian communication behaviour.

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