Anim. Behav., 1979, **27**, 173–184

DISPLAY BEHAVIOUR OF MALE *ANOLIS OPALINUS* (SAURIA, IGUANIDAE): A CASE OF WEAK DISPLAY STEREOTYPY

BY THOMAS A. JENSSEN

Biology Department, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061

Abstract. *Anolis opalinus* lacks even one discrete display pattern. Syntopic with as many as four congeners, *A. opalinus* contradicts the hypothesis that increased stereotypy of species-recognition displays is favoured among sympatric congeners. Head bobs (4 to 11) and dewlap pulses (0 to 8) varied per display. However, a re-occurring 'theme' was isolated which explained the variable bob cadences of most displays (75%). This theme was: (1) an initial double head bob series, (2) a middle bob series of successively quickening cadence, and (3) a final bob series of successively slowing cadence. Sixteen display-related parameters were examined for intra-display correlations; all but a few correlations were non-significant. The unusual *opalinus* display behaviour may have resulted from relaxed selection for stereotyped displays, with other features being used for mate selection and species recognition.

The most basic characteristics of lizard displays are their marked stereotypy and species-uniqueness (Carpenter 1967; Jenssen 1977). Although certain aspects of a lizard's displays may have a limited range of variability, there is a basic and predictable pattern of body movement through time which distinguishes any one display type from other display types within a lizard's repertoire and from the displays of other species (Jenssen 1977, 1978). The display behaviour of *Anolis opalinus* is a notable exception to this generalization.

Male *A. opalinus* lack even one discrete display pattern. Syntopic with several species of anoles on Jamaica, *A. opalinus* contradicts the attractive hypothesis that increased stereotypy of species-recognition displays is favoured among sympatric congeners.

Methods and Materials

Anolis opalinus is the smallest of the seven anoline species on Jamaica (Underwood & Williams 1959). It is widely distributed on the island, showing ethoecological flexibility when residing with different combinations of congeners (Jenssen 1973). The species' ecology and behaviour were studied in Jamaica from March 1970 to March 1971 and during the summers of 1971 and 1975. During this time I used a Nizo S80 camera and 2883 m of super 8 film to record *A. opalinus* social behaviour; from this film record 639 displays of good quality were selected as the data base for the present analysis. These displays were performed by 51 marked adult males of known size and weight (mean SVL 47·7 ± SD 4·5 mm; mean body wt 2·35 ± SD 0·63 g) from the following five localities: Anchovy (one male, 24 displays), located on the northwest part of the island, St. James Parish, 6·5 km south of Montego Bay; Crawford (five males, 127 displays), located on the southwest coast, St. Elizabeth Parish, 6 km west of Black River; Hellshire Hills (five males, 68 displays), located on the southeast coast, St. Catherine Parish, 12 km south of Spanish Town; Long Mountain (nine males, 81 displays), located on the southeast part of the island, St. Andrews Parish, 0·9 km southwest of the University of the West Indies, Mona (a suburb of Kingston); and Mandeville (31 males, 339 displays), located on the central part of the island, Manchester Parish, within Mandeville.

Several techniques were employed to film the displays in the field and in enclosures. For the 196 field-filmed displays, recordings were made by following naturally occurring behaviour of males as they moved about their territories, and by releasing an unrestrained male into another male's territory and filming the ensuing encounter.

For the 443 enclosure-filmed displays, males were placed singly into a wooden 1·3 (L) × 0·7 (H) × 0·4 (W)-m enclosure with a glass front. The enclosure contained mulch, limbs, vines, and epiphytes common to *opalinus* habitat. Two to four adult females were always in the cage. A second adult male was also present in the enclosure for a portion of the time during the filmed male's residency. Therefore, displays were performed during male–female and male–male interactions.

Displays were filmed at 18 frames/s. Only those displays known to be complete were used in the analysis. The resulting films were analysed frame-by-frame with a Kodak MFS Ektagraphic projector (see Jenssen & Hover 1976 for methodology).

Upon initial analysis, I was unable to detect even one stereotyped display pattern. Bob number, bob cadence, bobbing duration, appearance and number of dewlap pulses, and duration of dewlap pulsing were all quite variable between displays. To make sense out of the seemingly inconsistent display behaviour, I placed all available data for each display on IBM cards. On each card there were recorded: (1) the displayer's identification number; (2) home locality of the displayer; (3) snout-vent length of displayer to nearest 1·0 mm; (4) body weight of displayer to nearest 0·01 g; (5) the number of the film roll on which the display was recorded and which display on the roll it represented (e.g. 15–3 is roll 15, third display on roll); (6) the number of film frames which recorded each Inter-Bob Pause (IBP) of a display (an IBP is duration from the peak of an initial head bob to the peak of the next bob); (7) the number of head bobs in the display; (8) total duration of head bobbing (derived from summation of IBP durations); (9) number of frames between last head bob and first dewlap pulse; (10) number of dewlap pulses following head bobbing; (11) total duration of dewlap pulsing; (12) numbers and kinds of modifiers (e.g. crest up, gorged throat, protruded tongue, head cocked, and introductory movements) accompanying the display; (13) body parts used to produce the bobbing (i.e. neck muscles, forelimbs, all limbs); (14) social context in which the display occurred (i.e. not known, assertion or non-directed behaviour, male–male interaction, male–female interaction); (15) whether the display was performed in the field or in an enclosure, and (16) whether the display was performed singly or as one of several displays performed in a series (i.e. 'a volley'). From the IBM cards, descriptive statistics (mean, standard deviation of the mean and 95% confidence limits of the mean), correlation analyses, and tests of significance were run on appropriate data.

First Computer Analysis

Before computing the above statistics the data were searched for any possible re-occurring patterns. Since all bobs of a display were similar (Fig. 1), it was the relative durations between the bobs (Inter-Bob Pauses) which determined bob cadence and served as the major pattern-producing factor for a display. To facilitate detection of any re-occurring bob patterns, all IBP (inter-bob pause) durations of a display were converted to a percentage of the total duration of that display. This made all displays of equal length (i.e. 100%). The displays were next separated according to the number of bobs within each display; eight bob-number categories resulted (i.e. categories of 4-bob displays up to 11-bob displays).

A program was then implemented for an IBM 370 computer which took the first display of a bob-number category and designated it as a 'model'. The IBP percentages of the next display of the same bob-number category were compared to the corresponding IBP values of the model; if they matched the respective IBPs of the model (± 7%), the display was classified as being like the model; if one or more IBPs did not fall within the arbitrary limits, the display was rejected and it was designated as a second model. The program then examined the next display from the sample and matched it with the first model; if rejected, the display was compared with the second model; if rejected, the third display also became a model. In this way all displays of a bob-number category (e.g. all 7-bob displays) were sorted and grouped according to the relative proportion each IBP held within a display. A graphic representation of each model was provided by the computer on a CALCOMP plotter which included the number of displays incorporated into each model, the mean for each IBP within each model, and the standard deviation marked on each side of the corresponding IBP means.

The first computer analysis separated the 639 displays into 103 'models' or groups of displays having very similar bob cadences. From these I recognized a common theme running through

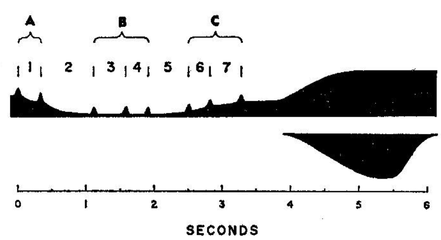

Fig. 1. A display-action-graph of an 8-bob display showing how the relative lengths of the inter-bob pauses (IBPs) describe bob cadence. The display is composed of three series of bobs: (A) initial double bob, (B) a second series of decreasingly spaced bobs, and (C) a third series of progressively spaced bobs. Head amplitude is depicted by the upper block and dewlap extension by the lower block.

most of the models which consisted of three series of bobs having certain characteristics: (1) displays began with a double bob; (2) could contain a middle series of bobs in which the successive IBPs decreased in duration (progressively faster rate of bobbing); and (3) finished with a final series of bobs in which the IBPs successively increased in duration (progressively slower rate of bobbing). Bobs of the middle series never numbered more than the bobs of the end series for a given display.

Most of the models which emerged from the first computer analysis fit into 12 generalized bob patterns which were formulated from the above theme (Fig. 2). I wrote 12 'rules', one for each of the 12 generalized bob patterns. Each rule specified only whether a particular IBP within its generalized pattern was longer or shorter than the neighbouring IBP (see Fig. 3). Each rule loosely described the bob cadence of a particular generalized pattern with no other constraints.

Second Computer Analysis

In the second computer analysis the 639 displays were sorted once more using the 12 rules (Table I). Any display which satisfied a particular rule for its bob-number category was 'explained'. The computer plotted a graph for each group of explained displays which included the mean IBP percentages and their standard deviations; a printout of the descriptive statistics (IBP means, standard deviation of the means, standard error of the means, and 95% confidence limits of the means) for displays expressed in real time and in per cent values was also provided.

Displays which did not conform to the rules were 'unexplained'. These residue displays were then processed by the program which controlled the first computer analysis. The computer-generated graphs of the models for unexplained displays permitted easy assessment of: (1) the number of displays of a bob-number category which deviated from the rules, (2) the kinds of display variations which deviated from the specified patterns, and (3) possible explanations of how the deviations were produced (e.g. critical lengthening or shortening of particular IBPs, or a head bob which may have been deleted by the lizard).

Results

The display analysis of *Anolis opalinus* is based on 639 filmed displays from 51 males, which represent five widely separated localities on

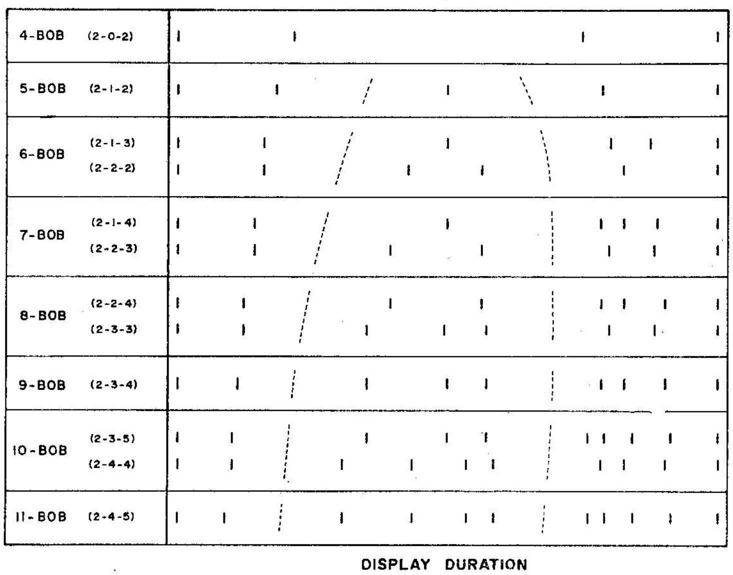

Fig. 2. Twelve generalized bob patterns which explain most *Anolis opalinus* displays. Bob cadence of each pattern is given within parentheses. Vertical lines represent bobs, and distances between vertical lines are inter-bob pauses (IBPs). Dotted lines separate each pattern into three series of bobs which correspond to divisions of bob cadence. Units of display duration are not given since patterns are hypothetical.

Jamaica. No stereotyped display pattern was found for this species either by locality or from the entire sample. The performance varied from four to 11 bobs per display (mean of 7·3 ± SD 1·4 bobs) and could have zero to eight dewlap pulses (extension and retraction of the dewlap) following the bobbing. The number of bobs per display and number of pulses per display for the entire sample were similar to a normal distribution and a Poisson distribution, respectively (Fig. 4).

Bob Patterns

Though no stereotyped bob pattern or patterns were evident in *A. opalinus*, the computer analyses did isolate an abstract theme (see Methods) which explained 74·8% of the bob cadences from my sample (Fig. 5). The bob pattern theme consisted of three bobbing series: an initial double bob, a middle series of bobs with a progressively faster rate of bobbing, and a final series of bobs where the rate of bobbing continually decreased.

Obviously 4-bob displays do not exhibit all aspects of the above theme; they only contain the initial double bob and two bobs of the final series (a 2–0–2 cadence). In the 5-bob displays, all three series are represented (a 2–1–2 cadence). In the 8-bob displays having a 2–3–3 cadence and displays with nine or more bobs, all aspects of the theme are expressed (i.e. the progressive change in rate of bobbing within the middle and end bobbing series).

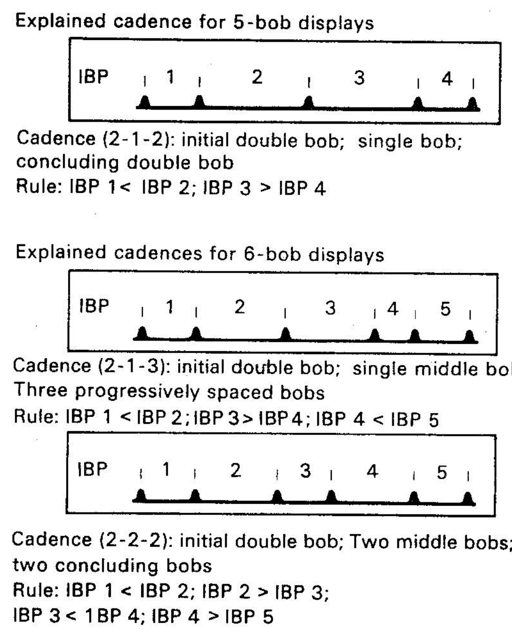

Fig. 3. Examples of explained 5- and 6-bob displays showing how bob cadence is separated into three series of bobs and how the rules for each pattern were derived.

Pattern Deviations

Twenty-five per cent of the displays did not satisfy the rules for explained bob patterns. These unexplained displays did not deviate greatly from the explained displays, and did not

Table I. Rules Governing Bob Cadence for 12 Generalized Bob Patterns of *Anolis opalinus* Displays. A Rule Only Dictates Whether an Inter-bob Pause (IBP) is Longer (>) or Shorter (<) than its Neighbour

4-bob displays
Rule for 2–0–2 cadence
IBPs: $1 < 2,\ 2 > 3$

5-bob displays
Rule for 2–1–2 cadence
IBPs: $1 < 2,\ 3 > 4$

6-bob displays
Rule for 2–1–3 cadence
IBPs: $1 < 2,\ 3 > 4,\ 4 < 5$
Rule for 2–2–2 cadence
IBPs: $1 < 2,\ 3 < 4,\ 4 > 5$

7-bob displays
Rule for 2–1–4 cadence
IBPs: $1 < 2,\ 3 > 4,\ 4 < 5,\ 5 < 6$
Rule for 2–2–3 cadence
IBPs: $1 < 2,\ 3 < 4,\ 4 > 5,\ 5 < 6$

8-bob displays
Rule for 2–2–4 cadence
IBPs: $1 < 2,\ 3 < 4,\ 4 > 5,\ 5 < 6,\ 6 < 7$
Rule for 2–3–3 cadence
IBPs: $1 < 2,\ 3 > 4,\ 4 < 5,\ 5 > 6,\ 6 < 7$

9-bob displays
Rule for 2–3–4cadence
IBPs: $1 < 2,\ 3 > 4,\ 4 < 5,\ 5 > 6,\ 6 < 7,\ 7 < 8$

10-bob displays
Rule for 2–3–5 cadence
IBPs: $1 < 2, 3 > 4, 4 < 5, 5 > 6, 6 < 7, 7 < 8, 8 < 9$
Rule for 2–4–4 cadence
IBPs: $1 < 2, 3 > 4, 4 > 5, 5 < 6, 6 > 7, 7 < 8, 8 < 9$

11-bob displays
Rule for 2–4–5 cadence
IBPs: $1 < 2, 3 > 4, 4 > 5, 5 < 6, 6 > 7, 7 < 8, 8 < 9, 9 < 10$

in themselves show any consistent patterns. To demonstrate this, deviant displays of the most represented bob-number category (7-bob) are presented (Fig. 6). Of the 272 7-bob displays, 39 did not produce a 2–1–4 or a 2–2–3 bob cadence shown in Figs. 2 and 5 for this bob-number category. The unexplained models in Fig. 6 show where the deviant display patterns vary from the two explained patterns.

The first three models of Fig. 6 deviate from the 2–1–4 cadence rule. The remaining four models deviate from the 2–2–3 cadence rule. In the first model an initial double bob is not apparent because the second bob (second vertical line) is closer to the third bob than to the first; this results in a 1–2–4 cadence. An explanation is that this may be an 8-bob display with a 2–2–4 cadence in which the lizards deleted the first bob. In the first three models of Fig. 6 the last bob series varies from the 2–1–4 cadence rule because the bobbing rate does not progressively decrease. The next three models deviate from the 2–2–3 cadence rule for the same reason. In the last model the 2–2–3 cadence is obscured because the last bob of the middle series is too close to the first bob of the end series.

The large standard deviations for the IBPs in Fig. 5 show how extremely variable the bob patterning is between explained displays of the same rule; there was a good chance that a randomly chosen display would deviate from its corresponding rule. This was especially true of

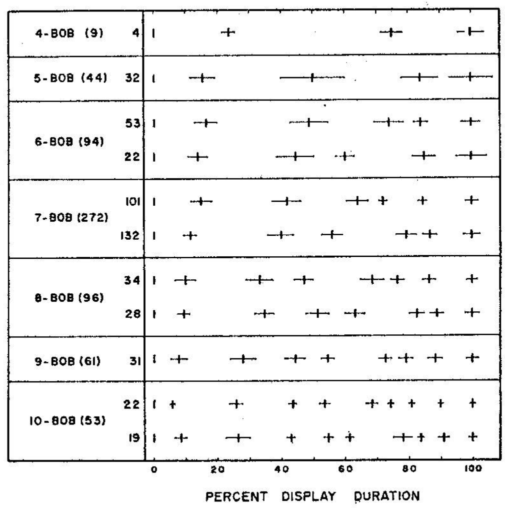

Fig. 5. Mean bobbing patterns generated from 478 displays that conformed to the rules of Table I. A vertical line indicates position of a bob and its concomitant horizontal line indicates the range for 68% of the variability (i.e. ± 1 SD) about the mean bob position. Total sample size for a bob-number category appears within parentheses (explained plus unexplained displays). Sample size for an explained pattern appears without parentheses.

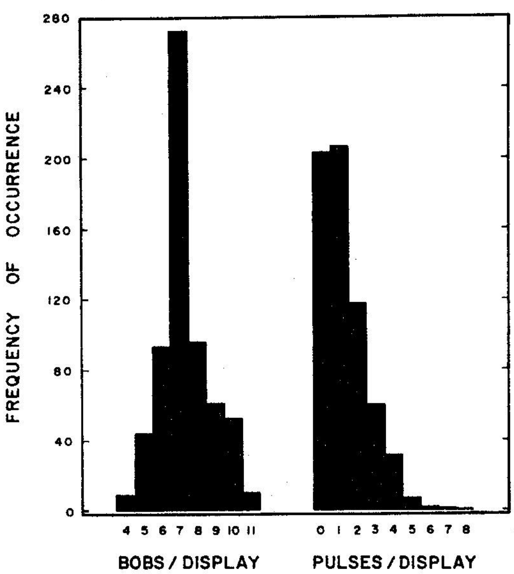

Fig. 4. Frequency distributions of bobs per display and dewlap pulses per display for 639 *Anolis opalinus* displays performed by 51 males.

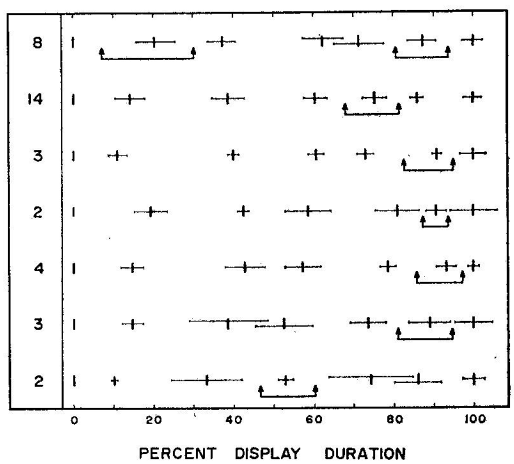

Fig. 6. Mean bobbing patterns of models for unexplained 7-bob displays. A vertical line indicates position of a bob and its concomitant horizontal line indicates the range for 68% of the variability (i.e. ± SD) about the mean bob position. Arrows locate the inter-bob pauses which deviated from the rules for 7-bob displays. Numbers represent sample sizes.

Table II. Descriptive Statistics (Mean, Standard Deviation, and Coefficient of Variation) of Total Duration of Bobbing, the Number of Dewlap Pulses Following Bobbing, and the Number of Modifiers Accompanying Each Display for the Eight Bob-number Categories (BNC) from 639 Filmed Displays of *Anolis opalinus*

BNC (N)	Bob duration (s) $\bar{x} \pm$ SD (CV)	Number of pulses $\bar{x} \pm$ SD (CV)	Number of modifiers $\bar{x} \pm$ SD (CV)
4-bob (9)	1·40 ± 0·54 (39%)	1·89 ± 1·05 (56%)	1·00 ± 1·12 (112%)
5 bob (44)	2·42 ± 0·72 (30%)	1·84 ± 1·55 (84%)	1·11 ± 1·08 (97%)
6-bob (94)	2·79 ± 0·95 (34%)	1·20 ± 1·35 (113%)	1·39 ± 1·31 (94%)
7-bob (272)	3·17 ± 0·93 (29%)	1·20 ± 1·29 (108%)	1·54 ± 1·20 (78%)
8-bob (96)	3·31 ± 1·06 (32%)	1·63 ± 1·39 (85%)	1·72 ± 1·32 (77%)
9-bob (61)	3·26 ± 1·06 (33%)	1·38 ± 1·54 (112%)	2·44 ± 1·53 (63%)
10-bob (53)	3·09 ± 0·91 (30%)	1·47 ± 1·51 (103%)	2·94 ± 1·77 (60%)
11-bob (10)	2·86 ± 0·89 (31%)	1·30 ± 1·63 (125%)	1·84 ± 1·69 (92%)

11-bob displays; none of the 10 analysed satisfied all the conditions of the 11-bob rule (Fig. 7). In the first two models shown in Fig. 7, each display deviates from its rule by the 'mis-timing' of only one or two bobs. The mean IBP values of the third model look as if the incorporated displays fit the specified pattern; yet each of the eight displays contained in this model had an errant IBP which disqualified it from the explained pattern. Since mean display durations were about the same for most bob-number categories (Table II), sloppy timing apparently becomes critical in the bob cadence of 11-bob displays.

Bob Characteristics

Total display duration for head bobbing averaged 3·06 ± SD 0·99 s, for the 639 analysed displays. The coefficient of variation (SD/$\bar{x}$ × 100) was 32·5%, indicating weak temporal stereotypy for display duration (Barlow, in press). This lack of stereotypy was even more

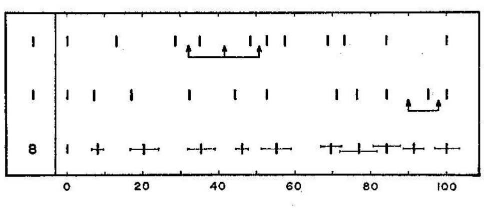

Fig. 7. Mean bobbing patterns of models for unexplained 11-bob displays. See legend of Fig. 6 for complete explanation of this figure.

apparent from the C.V. values of individual IBP durations which range from 29% to 90%. With this kind of variability there is little consistency to bob patterns (Table III).

The range of temporal variability was shared to a large degree by all 51 males of the sample. To demonstrate this, an analysis of variance (ANOVA) was run on display durations. The resulting ANOVA showed 82% of the variation came from the within groups component and only 18% from the among groups component.

There was a marked locality effect on the frequency distribution of bob number/display for some of the sampled populations (Fig. 8). Lizards from the western populations (Anchovy and Crawford) performed 9- and 10-bob displays more frequently than lizards from the eastern populations. To test this locality effect, the non-parametric χ^2 test for two independent samples (Siegel 1956) was used to compare the frequency distributions of bob numbers/display from the two western populations with that of the combined Mandeville, Hellshire Hills, and Long Mountain populations. The results showed a highly significant difference ($\chi^2 = 311{\cdot}4$, $df = 7$, $P < 0{\cdot}01$).

Any one lizard was just about as likely to perform the same range of bob numbers per display as any other lizard within a population group. This is reflected by the partitioned variance from ANOVAs run on the combined Anchovy & Crawford populations (95·0% within lizards, 5·0% among lizards) and the combined Mandeville, Hellshire Hills, and Long Moun-

Table III. Descriptive Statistics (Mean, Standard Deviation, and Coefficient of Variation) of Inter-bob Pause (in seconds) for the Eight Bob-number categories (BNC) from 639 Filmed Displays of *Anolis opalinus*

	Inter-bob pauses									
BNC	1	2	3	4	5	6	7	8	9	10
4-bob										
$\bar{x}$	0·488	0·525	0·383							
SD	0·375	0·238	0·174							
CV	77%	45%	46%							
5-bob										
$\bar{x}$	0·483	0·849	0·677	0·405						
SD	0·278	0·377	0·313	0·162						
CV	57%	44%	46%	40%						
6-bob										
$\bar{x}$	0·508	0·856	0·605	0·385	0·436					
SD	0·290	0·407	0·278	0·187	0·164					
CV	57%	48%	46%	49%	38%					
7-bob										
$\bar{x}$	0·432	0·877	0·597	0·497	0·333	0·450				
SD	0·183	0·337	0·239	0·264	0·168	0·293				
CV	42%	38%	40%	53%	51%	65%				
8-bob										
$\bar{x}$	0·357	0·730	0·527	0·590	0·381	0·339	0·401			
SD	0.166	0·274	0·245	0·293	0·218	0·263	0·142			
CV	46%	38%	46%	50%	57%	78%	36%			
9-bob										
$\bar{x}$	0·302	0·635	0·488	0·370	0·524	0·261	0·305	0·374		
SD	0·203	0·280	0·159	0·224	0·152	0·182	0·132	0·146		
CV	67%	44%	33%	61%	29%	70%	43%	39%		
10-bob										
$\bar{x}$	0·237	0·569	0·486	0·340	0·360	0·297	0·227	0·268	0·301	
SD	0·121	0·203	0·192	0·128	0·188	0·172	0·166	0·100	0·102	
CV	51%	36%	40%	38%	52%	58%	73%	37%	34%	
11-bob										
$\bar{x}$	0·244	0·350	0·394	0·322	0·250	0·378	0·228	0·228	0·211	0·256
SD	0·092	0·183	0·121	0·119	0·146	0·150	0·182	0·205	0·073	0·142
CV	37%	52%	31%	37%	59%	40%	80%	90%	35%	55%

tain populations (78·2% within, 21·8% among lizards).

A lizard's home locality, however, had no effect upon display duration. Regardless of the number of head bobs in a display, the mean duration for the bobbing sequence was about the same (Table II); only 4- and 5-bob displays were noticeably quicker.

Pulse Characteristics

In 68% of the displays (436/639), pulsing of the dewlap followed the head bobbing portion of the display. The interval between the last head bob and the first dewlap pulse was quite variable ($\bar{x} = 0{\cdot}68 \pm$ SD 0·5 s, C.V. = 74%).

The number and duration of pulses following head bobbing was extremely variable, too. Frequency distribution of pulse number/display resembled a Poisson distribution (Fig. 4) which indicates a randomly occurring event (Batschelet 1971, p. 385). There was a mean of 2·0 pulses/display for displays with one or more pulses. The analysis of variance demonstrates that each lizard was just as likely to vary the number of pulses in its display as any other lizard (88% variation within lizards, 12% variation between lizards).

The frequency distribution of pulse numbers/display was about the same for all five localities (Fig. 8). The mean duration of dewlap pulsing was 4·92 ± SD 3·78 s. In displays having several dewlap extensions and retractions, the last pulse tended to be slower than the initial pulses.

Intra-display Correlations

The various elements of the *opalinus* display showed wide variability. This low level of stereotypy may be considered 'noise' in the signal and be biologically irrelevant, or the variability may serve to communicate information via a graded signal. If the latter viewpoint is true, there should be certain events within the display which co-vary. Below, a number of display aspects are examined to evaluate which viewpoint is best supported for *A. opalinus* display behaviour.

(1) The number of bobs per display was only weakly correlated with display duration ($r = 0{\cdot}206$).

(2) The number of bobs per display varied independently of both the number of pulses ($r = 0{\cdot}000$) and pulse duration ($r = 0{\cdot}006$).

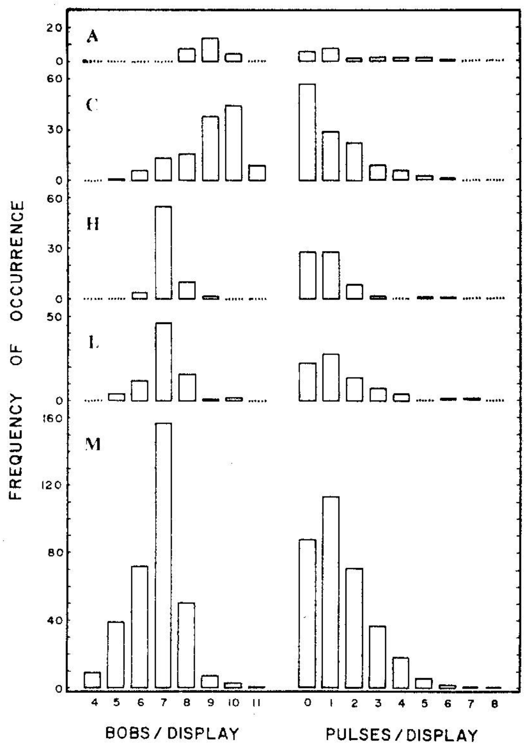

Fig. 8. Frequency distributions of bobs per display and dewlap pulses per display for 639 *Anolis opalinus* displays by one male from Anchovy (A), five males from Crawford (C), five males from Hellshire Hills (H), nine males from Long Mountain (L), and 31 males from Mandeville (M).

(3) There was no statistically significant correlation between the duration of head bobbing and the number of pulses ($r = -0{\cdot}024$), or between bob duration and pulse duration ($r = 0{\cdot}029$) in a display. The absence of a correlation between these two prominent display features (bobbing and dewlap pulsing) was surprising.

(4) Neither snout-vent length nor weight of a male co-varied significantly with display duration ($r = 0{\cdot}006$ and $0{\cdot}019$, respectively) nor with the number of pulses in a display ($r = -0{\cdot}058$ and $-0{\cdot}067$, respectively). Thus, the temporal display characteristics of smaller adult males were not any different from those of larger males.

(5) A correlation between body size and bobs/display for males of Hellshire Hills, Long Mountain, and Mandeville was not significant ($r = 0{\cdot}025$). The six males from Crawford and Anchovy were deleted from this correlation as they were large males, and animals from these populations tended to have more bobs/display.

(6) No significant correlation was found between number of static modifiers appearing with a display (an index of relative arousal) and display duration ($r = 0{\cdot}032$) or between number of static modifiers and number of pulses in a display ($r = 0{\cdot}042$).

(7) The only statistically significant correlation ($P < 0{\cdot}01$) was between the number of bobs in a display and the number of static modifiers accompanying the display ($r = 0{\cdot}305$); males who were aroused tended to perform more bobs/display.

To look at this statistically significant correlation from another perspective, I took 270 displays performed in the field by Mandeville males (113 filmed displays and 157 displays recorded in my field notes) for which social contexts were known. The social contexts were assertion (non-directed displays during which males are least likely to be aroused), male–female (primarily courtship directed displays), and male–male (social interactions in which males are most likely to be aroused). The resulting frequency distributions for number of bobs/display and number of pulses/display within assertion and male–female contexts were similar (Fig. 9). Only in the male–male encounters was there the slightest tendency for displays to have more bobs and pulses than in the other two contexts. However, the mean number of bobs/display for each context (assertion, 6·6;

male–female, 6·6; male–male, 6·9) was about the same. The differences in the frequency distributions between the three social contexts of Fig. 8 are not sufficient to explain the variable numbers of bobs and pulses appearing in *opalinus* displays.

Present data indicate that the variability within *opalinus* displays may be considered 'noise' in the signal. There is little to suggest that the display variability is systematically being used to convey information.

Display Volleys

During contexts of significant social interactions such as courtship, copulation, and prolonged territorial disputes, males were observed performing displays in quick succession. When displays were performed in 'volleys', the body and head attitudes were not changed between displays. One hundred and eighty-four displays of my sample (29 %) were performed in volleys. Seventy per cent of the 77 volleys consisted of two displays, while 22 % of the volleys contained three, 7 % contained four, and 1 % contained five displays.

When displays appeared in volleys, the duration of head bobbing in each subsequent display was shorter than the bobbing duration of the preceding display. In volleys having two displays, first displays of the sample averaged 3·21 ± SD 1·01 s per bob duration and the second display of the volley had a mean bob duration of 2·38 SD 0·67 s. A Wilcox matched-pairs signed-rank test (Siegel 1956) verified that the second display of a volley was shorter than the first ($z = 3{\cdot}84$, $P < 0{\cdot}01$).

In slightly more than half of the volleys (54 %) the number of bobs in both displays was the same; in 32 % of the volleys there were one to two more bobs in the first display than in the second, and in 14 % of the volleys the reverse was true.

One of the few correlations with the number of pulses following head bobbing involved volleys. For 70 % of the volleys, there was a single dewlap pulse in all displays of a volley, except for the last display which was concluded by two to seven pulses ($\bar{x} = 3{\cdot}1 \pm$ SD 1·16). The multiple pulsing at the end of the terminal display of a volley might be interpreted as signalling the conclusion to the chain of displays.

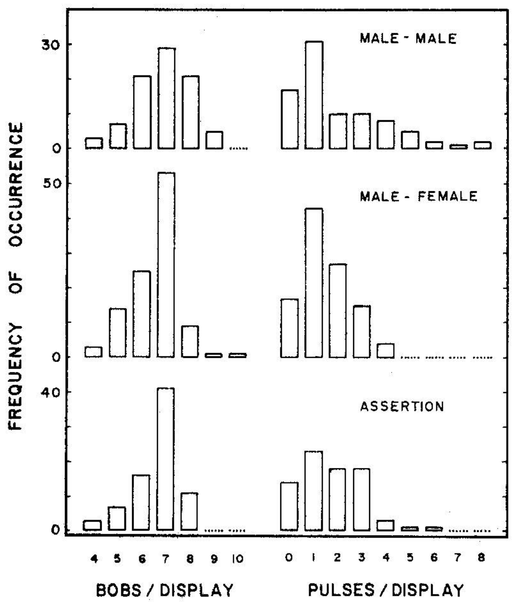

Fig. 9. Frequency distributions of bobs per display and pulses per display for 270 *Anolis opalinus* displays performed in the field by Mandeville males, and grouped by social context.

Use of the Generalized Patterns and Unexplained Models

Except for the majority of 9- and 10-bob displays being performed by lizards from Anchovy and Crawford, there was no evidence of populations performing a different combination of the 12 generalized patterns for explained displays.

The next consideration was whether individuals exclusively used just a few of the possible explained and unexplained bob cadences. To test this idea, a sample of 10 males for which there were a large number of recorded displays (16 to 45) was analysed for the kind and frequency of bob cadences performed. Nineteen classes of bob cadences were established, being made up of the explained generalized pattern(s) (1, or 1 and 2) and the combined unexplained models for each bob-number category (Table IV). Together, the 10 lizards performed displays from 18 of the 19 classes of bob cadences. Each lizard for which I had the most observations performed almost half (nine) of the possible explained and unexplained bob cadences, while those with fewest observations had the least number of cadences (four) recorded for them (Table IV). On the average, each lizard used 6·4 different kinds of bob cadences; presumably, this average would be larger if the sample of

Table IV. The Frequency with which 10 *Anolis opalinus* Males from Crawford (C), Long Mountain (L), and Mandeville (M) Performed Displays of Explained Cadences (Expl. 1 or 2) and Unexplained Cadences (Unexpl.) Within the Eight Bob-number Categories

Bob pattern	Males									
	1(C)	2(L)	3(M)	4(M)	5(M)	6(M)	7(M)	8(M)	9(M)	(10)M
4-bob										
Expl. 1								1		
Unexpl.				1	2					
5-bob										
Expl. 1			5	3	1					1
Unexpl.				2	2					
6-bob										
Expl. 1		1		8	10		1	3		2
Expl. 2	1			1	1	2	2		1	
Unexpl.		1			3			1	1	1
7-bob										
Expl. 1	8		8	11	9	2	2	17	7	7
Expl. 2		16	6	3		5			13	3
Unexpl.		1	1		4	2	1		3	
8-bob										
Expl. 1	2			3					3	
Expl. 2	2						6	7		2
Unexpl.						6	3			
9-bob										
Expl. 1	10									
Unexpl.	1					1	3			
10-bob										
Expl. 1	16									
Expl. 2	3									
Unexpl.	2				1	1			1	
11-bob										
Unexpl.										

displays for each individual was larger. There was no evidence for individual-specific usage of particular bob cadences as a possible cue for individual recognition.

A final consideration was whether the two explained bob cadences which appear within some of the bob-number categories have different numbers of pulses at the end of their respective displays. Using 6-, 7-, 8-, and 10-bob displays, almost the same frequency distributions of pulse numbers resulted when comparing the displays of both cadences within a bob-number category (χ^2 test for two independent samples; Siegel 1956; $\chi^2 = 1{\cdot}08$, $P = 0{\cdot}9$).

Discussion

In contrast to other iguanid lizards whose display behaviour has been studied, there are remarkably few aspects of *A. opalinus* displays that show a semblance of predictability. Each lizard species, or at least each population, is expected to have a signature display (i.e. a species-typical, stereotyped display pattern used during assertion and other contexts, see Jenssen 1977, 1978). However, for *A. opalinus* I have avoided the term signature display when referring to its head bobbing display behaviour, because of the lack of a discrete display pattern that might characterize this species.

The possibility occurred to me that *A. opalinus* might have a repertoire of several stereotyped, but similar display patterns that were confusing the analysis. This is not the situation. There exist large standard deviations and C.V. values for the IBPs of all explained and unexplained bob patterns (Table II and Figs. 4, 5 and 6), whether the data are expressed in real time or per cent durations. If there were a number of discrete stereotyped patterns, they would have been detected and separated by the initial computer run (see Methods).

If *A. opalinus* has several display types of similar patterning, one would expect that the various features of dewlap pulsing would serve as cues to these patterns by correlating in different ways with the observed head bobbing characteristics. For example, 4-bob displays might have fewer dewlap pulses than 8-bob displays. However, no such correlations exist to suggest separate display types. Another way to uncover a multiple display repertoire is to examine the characteristics of displays performed within different social contexts. If there are several discrete patterns, they would probably have different information content and would be used in distinctive manners. Again, no specific display patterns or display features correlated with particular social situations. *Anolis opalinus* presents no evidence that it has a repertoire of several discrete display types, nor that it possesses a single display pattern which one might label as the species' signature display.

Rather than retreat entirely from the concept of species-unique display behaviour and state that *A. opalinus* never had a stereotyped signature display, I suggest the following alternative. During speciation and concomitant radiation of Jamaican anoles, the progenitor of *A. opalinus* may have had stereotyped display behaviour; since that time, however, selection pressure for maintaining display stereotypy has relaxed for *A. opalinus*. That *opalinus* displays do not appear to be under strong selection pressure comes from the following observations: the frequency of occurrence for bob number per display has a wide range (4 to 11 bobs), and these head bob displays do not have discrete stereotyped pattern or patterns (Figs. 2, 4 and 5). Any lizard of a population appears capable of performing this range of bob-number variability. Furthermore, I could find few correlations between the numerous display events analysed, indicating that the variability is not important in communication. Finally, one of the most enigmatic of *opalinus* display features is dewlap pulsing. Besides a weak correlation between multiple pulses and the end of a volley, the occurrence of pulsing following head bobbing seemed random.

The natural selection maintaining display stereotypy relates to display function. One function commonly ascribed to a species' signature display is that of species-recognition which is a major criterion used by females during mate selection (Crews 1975; Hunsaker 1962; Jenssen 1970). Theoretically, females that use the behaviour of males for mate selection would increase their fitness if they could detect some consistent species-unique trait in the display of a courting conspecific male, and thereby avoid investment in non-viable or uncompetitive hybrids. Thus, females would act as agents of natural selection for increasing the predictability and uniqueness of their species' display characteristics.

Yet predictability, as mentioned above, is not an obvious feature of *opalinus* displays, nor is species-uniqueness well developed. The *opalinus* display has not diverged much from those of *A. grahami* and *A. garmani*, the nearest relatives of *A. opalinus*. All three species, which are sympatric, have yellow-orange dewlaps, and the *grahami* and *garmani* displays are similar in structure to *opalinus* displays. They are comprised of five to eight bobs with or without a following series of dewlap pulses (Jenssen 1977).

I believe a major impetus for stereotypy (i.e. mate selection) has been deleted from *opalinus* display functions. Likely substitutes used for species recognition and mate selection are the characteristics of male body morphology and colouration. *Anolis opalinus* is Jamaica's smallest anole, verging on dwarf status (Williams 1972), and brown in colour. *Anolis grahami*, a stout lizard of intermediate size, has an aqua head, yellow-brown sides, and a magenta tail. *Anolis garmani* is the giant of Jamaican anoles and is a vivid green colour (Underwood & Williams 1959). One might speculate that during the initial evolution of ancestral stock leading to the speciation of *A. opalinus*, *A. grahami*, and *A. garmani* (though this was probably not a simultaneous event), differentiation between forms began primarily at the level of body morphology and colouration rather than with display behaviour.

Assuming stereotypy in the displays of *A. opalinus* in its evolutionary past, the data suggest that there may have been two display patterns of seven bobs each. Seven bobs is suggested by the modal number of bobs performed by most of the populations studied. The speculation that the early *opalinus* repertoire may have contained two stereotyped display patterns comes from two observations. First, there are two explained patterns which appear in 6-, 7-, 8-, and 10-bob displays, and second, both *A. grahami* and *A. garmani* have two display types in their repertoires (Jenssen 1977).

In summary, *opalinus* head bobbing displays probably have a communication function for the species, but that function is not obvious to me.

Acknowledgments

I am most grateful to the following people. Jeff Watkins and Gray Williams assisted me with the tedious task of analysing films. Roger Gledhill wrote the computer programs. Mr and Mrs F. Collins, Dr and Mrs J. H. Frank, and Dr and Mrs G. Mais of Mandeville gave me access to their properties and friendship, while tolerating the eccentric behaviour of a field biologist who painted their lizards. Without the following financial support this research opportunity would not have been possible: NIMH (postdoctoral fellowship 6FO2M4 33435-01A1 to T. A. Jenssen) and NSF (grants BMS 74-20143 to T. A. Jenssen and B 019801X to E. E. Williams.) I am also indebted to Risa Jenssen, A. Stanley Rand, David West, and anonymous reviewers for providing valuable criticism of the manuscript, and to Pam Hollandsworth for typing the manuscript.

REFERENCES

Barlow, G. W. In press. Modal action patterns. In: *How Animals Communicate* (Ed. by T. A. Sebeok). Bloomington, Ind.: University of Indiana Press.

Batschelet, E. 1971. *Introduction to Mathematics for Life Scientists.* New York: Springer-Verlag.

Carpenter, C. C. 1967. Aggression and social structure in iguanid lizards. In: *Lizard Ecology: A Symposium* (Ed. by W. Milstead), pp. 87–105. Columbia: University of Missouri Press.

Crews, D. 1975. Effects of different components of male courtship behaviour on environmentally induced ovarian recrudescence and mating preferences in the lizard, *Anolis carolinensis. Anim. Behav.*, **23**, 349–356.

Hunsaker, D. 1962. Ethological isolating mechanisms in the *Sceloporus torquatus* group of lizards. *Evolution*, **16**, 62–74.

Jenssen, T. A. 1970. Female response to filmed displays of *Anolis nebulosus* (Sauria, Iguanidae). *Anim. Behav.*, **18**, 640–647.

Jenssen, T. A. 1973. Shift in the structural habitat of *Anolis opalinus* due to congeneric competition. *Ecology*, **54**, 863–869.

Jenssen, T. A. 1977a. Evolution of anoline display behavior. *Am. Zool.*, **17**, 203–215.

Jenssen, T. A. 1978. Display diversity of anoline lizards and problems of interpretation. In: *Behavior and Neurology of Lizards: An Interdisciplinary Conference* (Ed. by N. Greenberg & P. MacLean), pp. 269–285. Rockville, Maryland: N.I.M.H.

Jenssen, T. A. & Hover, E. L. 1976. Display analysis of the signature display of *Anolis limifrons* (Sauria: Iguanidae). *Behaviour*, **57**, 227–240.

Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences.* New York: McGraw-Hill.

Underwood, G. & Williams, E. E. 1959. The anoline lizards of Jamaica. *Bull. Inst. Jamaica*, Sci. Ser., **No. 9**, 5–48.

Williams, E. E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. In: *Evolutionary Biology* (Ed. by T. Dobzhansky, M. Hecht & W. C. Steere), Vol. 6, pp. 47–89. New York: Appleton-Century-Crofts.

(*Received* 4 *February* 1977; *revised* 6 *June* 1977; *MS. number:* A1988)