

DISPLAY REPERTOIRE ANALYSIS OF *SCELOPORUS UNDULATUS HYACINTHINUS* (SAURIA: IGUANIDAE) FROM SOUTH-WESTERN VIRGINIA

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Abstract. *Sceloporus undulatus hyacinthinus* display behaviour was studied in the field and laboratory. Four major conclusions emerged. First, 'jiggling' seems to be a generalized behaviour appearing in many contexts with no apparent specialized function. Second, there are two distinct display types (A and B) in the species' repertoire besides jiggling. Third, based on 177 video-taped displays by 11 males, each of the two display types was extremely stereotyped. Last, the stereotypy is of two kinds. For the A displays, all males performed a display pattern common to the population (intra-population stereotypy); this would structure the behaviour for a species recognition function. For the B display, each male performed a consistent pattern. However, each male's B displays were to a lesser or greater extent individually unique (intra-individual stereotypy); this would facilitate individual recognition. Some males' B displays showed sufficient pattern variation to make it impossible to present a single display pattern representing the type B pattern for the population.

Investigations of iguanid lizard display behaviour have generally ascribed to these animals limited repertoires of stereotyped displays (see Jenssen 1975, p. 48 for references). Besides the inter-specifically similar 'jiggling' (Evans 1938; Ruibal 1967) accompanying male courtship behaviour, only a single species-unique 'assertion-challenge' display pattern has been reported by most investigators for their studied species.

However, recent investigations have revealed that several species of *Anolis* and a close relative, *Phenacosaurus heterodermus*, exhibit complex repertoires consisting of two or more species-unique display types (Stamps & Barlow 1973; Crews 1975; Jenssen 1975; Hover & Jenssen 1976; Jenssen & Rothblum 1977). The question arises whether the capacity for multiple display repertoires is restricted to anoles, or whether this phenomenon may be a more widespread characteristic of iguanid lizards.

The present study of the northern fence lizard (*Sceloporus undulatus hyacinthinus*) extensively quantifies the species' display behaviour and demonstrates that this species has a multiple display repertoire. These data support the possibility that non-anoline iguanid lizards may also have larger repertoires than previously suspected.

Methods

Observing, filming, and video taping the behaviour of 39 *S. u. hyacinthinus* were conducted under field and laboratory conditions from July until mid-September 1975. The population

studied resided in and around an abandoned coal-mining area situated in a pine forest 10 km north-west of Blacksburg, Montgomery County, Virginia.

Approximately 90 h were spent in the field observing the behaviour of 21 animals. During this period, 152 m of film were exposed, documenting the display behaviour of 12 males and 1 female under natural conditions. These field data were collected to verify that laboratory conditions were not causing a change in the lizards' normal behaviour, and to gain greater insight into the social contexts in which the various behaviours occurred. Displays filmed in the field were taken with a Nizo S80 camera set at a filming speed of 18 frames/s, but these films were not included in the final display analyses since equipment in the laboratory allowed for far greater precision in measuring display durations.

In the laboratory, 177 video-taped displays from 11 males were recorded and statistically analysed. Nine females were also under observation, but they displayed so infrequently that their behaviour is not included in this report. Display data from captive males were collected within two months of each lizard's capture.

The lizards were brought into an air-conditioned laboratory (24 to 26 C) and housed in 1.3 m (L) × 0.7 m (W) × 0.6 m (H) wooden enclosures fitted with a glass front panel and screen top. Double fluorescent light fixtures immediately overhead provided illumination; they were controlled by a timer set for a 12-h

photoperiod (06.30 to 18.30 hours). Inside the home cages were tree trunks, artificial foliage, and a moss-soil substrate scattered with leaves and twigs. No more than two females and two males were ever housed together in a single cage; normally the enclosures contained one male and a female. The lizards were identified with a coded series of non-toxic paint marks on their dorsa. Food (baby crickets and mealworms) and water for the animals were supplied daily.

A 2.6 m (L) \times 0.7 m (W) \times 0.6 m (H) wooden enclosure with slanted glass front panels and screen top was used as the observation/filming chamber throughout the study. A 0.8 m (W) \times 0.7 m (H) panel could be inserted to divide this enclosure in half (Fig. 1). Each compartment was outfitted and maintained in the same manner as the home cages. Normally, one male was placed in each compartment and, after 1 to 2 days, the centre insert was lifted and the resulting interactions filmed. Variations of this procedure were occasionally used in which one to two females were also placed in the enclosure or a third male was introduced as an 'intruder' during the observation periods.

To record and analyse the displays, a JCV video camera (GS2500) fitted with a Fujinon 12.5-100-mm zoom lens was used for video taping. An Odetics G-77 Video-Date Time Generator provided a timing signal in 0.01 s increments. The camera and date-time generator outputs were channelled into a Sanyo VTR 1200 video tape recorder having a frame-by-frame playback capability. The resulting video-taped displays were then replayed frame-by-frame (60 frames/s) into a Sony 19-inch monitor. Each analysed frame (representing increments of 0.017 s) contained a superimposed image of the date and elapsed time from the beginning of the 60-min tape. The head amplitude of a displaying lizard on each video tape frame was determined

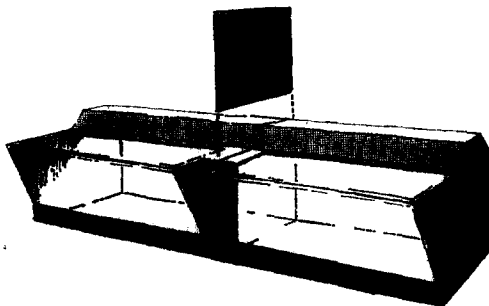


Fig. 1. Observation chamber showing sliding partition.

using a gridded transparent overlay placed across the TV monitor.

Two different displays (types A and B) were recognized during the observations. To facilitate analysis, these displays were artificially divided into 11 units which delineated the held portions of the first six bobs ('plateaus') and five inter-bob pauses (Figs. 2 and 3). The rapid ascending and descending movements of the bobs were not statistically analysed. Descriptive statistics on unit duration (mean, standard error, 95 and 99% confidence intervals) were calculated on each of the 11 units for every individual's type A and B displays. The same statistics were also calculated using the mean unit durations from each of the 11 males to estimate population variance for display variability. One-way analysis of variance (ANOVA) tests were run for each of the 11 units to determine the intra-individual (within) and inter-individual (among) variance components in both the Type A and B displays. Coefficient of variation (CV) was calculated ($SD/\bar{x} \times 100$) for the 11 units to give an estimate of relative stereotypy, where stereotypy increases as CV values decrease. (See Barlow *in press* for discussion.)

Results

Display Repertoire

Two distinct display types (A and B) were performed by all 11 male *S. u. hyacinthinus* in the laboratory and were verified by field observations and field-filmed displays. The two displays superficially resemble each other (Figs. 2 and 3). Their similarities are as follows: (1) both display types are extremely stereotyped in their temporal

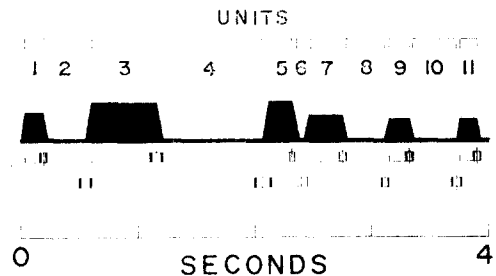


Fig. 2. Generalized type A display pattern calculated from 98 displays from 11 male *S. u. hyacinthinus*. Vertical axis of graph depicts relative head amplitude movement and horizontal axis gives display duration. Unit statistics are shown below graph: horizontal line: unit duration; vertical line: unit mean; outer edges of white boxes: 95% confidence intervals of unit mean; and outer edges of black boxes: 99% confidence intervals of unit mean.

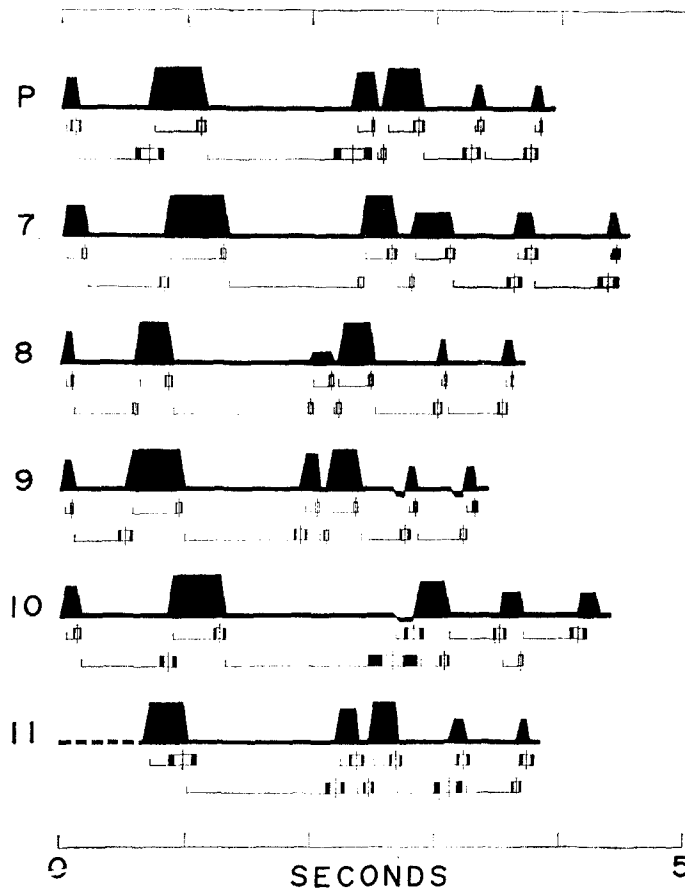


Fig. 3. Generalized type B display pattern calculated for displays pooled from six male *Sceloporus undulatus hyacinthinus* (P) having the same pattern, and five type B display patterns for individual male *S. u. hyacinthinus* (males 7-11) having individually unique patterns. Data based on 79 displays with unit statistics as in Fig. 2.

sequencing (Figs. 2 and 3); (2) they are similar in patterning, consisting of a series of 'plateaued' bobs and inter-bob pauses; (3) they were always performed through the fourth bob (unit 7), but showed a variable number of total bobs (total number of bobs within a display showed $\bar{x} = 8.1 \pm \text{SE } 0.2$ and range of 5 to 18 for A displays, and $\bar{x} = 8.7 \pm \text{SE } 0.4$ and range of 4 to 18 for B displays); (4) for a given display there were no significant differences between the lengths of inter-bob pauses past unit 8 nor between any plateaus past unit 9 giving the impression of a variable number of identical repetitions of the fifth bob (unit 9); (5) both display types could show a gradation in push-up amplitude from one display to the next, varying

from subtle head movements to full extension of all four legs; and (6) there was no correlation between display type and magnitude of leg extension during bobbing, or between total number of bobs in a display and magnitude of leg extension during bobbing.

A major distinction between the two display types was the temporal patterning of the bob plateau and inter-bob pause durations. The type B differed from the type A displays in that, for any given male, the bob plateaus of his type B displays were of shorter duration and the inter-bob pauses of longer duration than the corresponding units of his type A displays. Almost all of these A to B unit comparisons were statistically significant (Table I). An example of a

Table I. Comparison of Type A and Type B Displays for Each Male and for Data from All Males (T) to Show Which Male's Type A Unit Durations Are Statistically Different from his Corresponding Type B Unit Durations: (NS) Depicts Non-significant, $P > 0.05$; (*) Depicts Significant, $P < 0.05$; and () Depicts Highly Significant, $P < 0.01$**

Male	Units										
	1	2	3	4	5	6	7	8	9	10	11
1	**	**	**	**	**	NS	*	*	**	*	**
2	*	**	**	**	NS	NS	*	*	*	*	**
3	**	**	**	**	**	NS	**	*	**	NS	**
4	**	**	**	**	**	NS	*	*	**	NS	**
5	**	**	**	**	**	NS	**	NS	**	NS	**
6	**	**	**	**	**	NS	*	*	**	NS	**
7	**	**	**	**	**	NS	**	**	**	NS	NS
8	**	**	**	**	*	NS	NS	*	*	NS	*
9	**	**	**	**	*	NS	**	**	**	*	**
10	**	**	**	**	**	NS	**	*	**	NS	**
11	**	**	*	*	NS	NS	NS	NS	*	**	**
T	**	*	**	**	**	NS	*	*	**	NS	**

consistent diagnostic difference between A and B displays is the ratio resulting from a display's unit 2 duration/unit 3 duration; with the exception of only one display, this ratio always was less than 1 for A displays and greater than 1 for B displays (Fig. 4).

Type A Characteristics

The type A display pattern was held in common by all tested males of the population (intra-population stereotypy). Every male performed the same pattern consistently without any significant differences in temporal duration of the display's units. Because no distinctive individual differences were evident, the mean unit durations from each lizard's displays were pooled to yield a single display pattern (Fig. 2). As a measure of temporal stereotypy, note the narrow 99% confidence intervals for the A display units (Fig. 2).

The amplitude for the third and fourth bobs of the A displays also showed a consistent relationship, with the third bob being taller than the fourth. To demonstrate this relationship, a ratio was calculated by dividing the third bob amplitude by the fourth bob amplitude from each A display. For each male, a mean ratio was computed. All 11 means were greater than 1; the lower 95% confidence interval for each of these means was also greater than 1 for 9 of the 11 males.

The relative amount of variability in the A display is reflected by coefficient of variation (CV) values. The small CV values of 7% total display duration and 9 to 15% for all but the shortest unit durations quantify the extreme

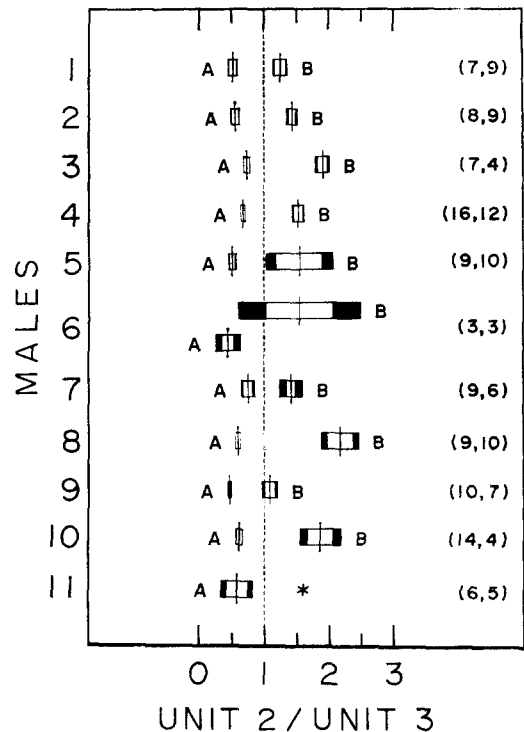


Fig. 4. Descriptive statistics of a diagnostic ratio (unit 2 duration / unit 3 duration) which differentiates type A displays (A) from type B displays (B) of *S. u. hyacinthinus*. Ratio statistics are depicted as: vertical line: ratio mean for a male; outer edges of white boxes: 95% confidence interval for mean; and outer edges of black boxes: 99% confidence intervals for mean. Numbers inside parentheses give individual male sample sizes for his A and B ratios. Star (*) indicates male 11 who had no unit 2 in his B displays.

stereotypy of this behaviour. Of the variability present, most was attributed to the among-lizard component (i.e. inter-individual variability), with only 10 to 37% of the unit variability being represented by variation within each lizard's displays (Table II). Since these displays are so consistent for the population as well as for each lizard, it is doubtful whether the proportionment of display variability among and within lizards has any significant communicative value. Therefore, based on its strong intra-population stereotypy, the A display probably functions as a species recognition signal.

Type B Characteristics

The B displays of any one lizard were, like his A displays, extremely stereotyped. The units composing a male's B displays, except for the shortest units, showed little temporal variability. The CV values for the unit durations of each male's displays were usually less than 11%, with CV values of 1 to 13% for total display duration for each of the 11 males. Of the temporal variability present, partitioning of variance showed that most of the unit variability occurred when comparing between displays of different lizards; in all but two units, the within-individual variation was less for the B displays than for the A displays (Table II).

The B displays exhibit a characteristic previously undescribed for any lizard species. While the A display epitomized intra-population stereotypy, the B displays demonstrated marked intra-individual stereotypy. Each male had his

own individual-unique B display. For six of the males, the consistent differences were very subtle and only involved small variations in unit durations which did not disrupt the pattern held in common by these males; identifying a display by means of his display required frame-by-frame analysis and could not be done when watching the display in real time. The display data for these six animals (males 1-6) were pooled (P) and used as a base for representing a generalized type B display pattern (Fig. 3). However, five animals (males 7-11) had B displays which contained significant differences in their patterns as compared with the B display pattern of males 1-6 (Fig. 3). Having males each with his own individual-unique B display pattern made it impossible to present a single pattern for the type B display of our *S. u. hyacinthinus* population.

The variations by which the B displays of males 7-11 deviated from the pooled B displays consisted of: (1) accentuated amplitude differences between adjacent bobs and (2) bob deletion. The deviations from the pooled pattern were readily detectable by an observer watching the animals display and could be used to identify the displayer. By way of example, the type B display of male 7, in addition to being comparatively slow, had a much higher amplitude to its third bob than its fourth; the third bob amplitude/fourth bob amplitude ratio had a 95% confidence interval of 1.51 to 2.04 and was by far the largest ratio value for any of the 11 males. Male 8, in contrast, had a very low

Table II. Proportion of Variance Found Within Groups (Intra-individual Variability) and Among Groups (Inter-individual Variability) Resulting from Single Classification Analysis of Variance Applied to Unit Durations of 98 Type A and 79 Type B Displays from 11 Male *Sceloporus undulatus hyacinthinus*

Unit	Variance partitioning			
	A		B	
	Within	Among	Within	Among
1	34.36	65.64	07.17	92.83
2	41.77	77.53	03.59	96.41
3	29.68	70.32	25.10	74.90
4	21.63	78.37	11.04	88.96
5	43.10	56.90	27.92	72.08
6	10.98	89.62	24.04	75.96
7	29.05	70.95	24.13	75.87
8	32.27	67.73	28.99	71.01
9	37.12	62.88	22.83	77.17
10	26.29	73.71	22.07	77.93
11	27.84	72.16	38.17	61.83
Entire display	33.43	66.57	27.92	72.08

amplitude third bob; the resulting amplitude ratio for bob 3/bob 4 had a 95% confidence interval of 0.18 to 0.25. The unique feature of male 9 B displays was 'dips' immediately preceding bob 5 and other subsequent bobs. Males 10 and 11 were both distinguished by B displays which did not contain all of the units performed by the other lizards. Male 10 did not perform the third bob and male 11 deleted the first bob from his pattern (Fig. 3).

In contrast to the proposed species-recognition function of the A display, the B display seems structured to potentially convey individual recognition. Each male's B displays were very stereotyped, while showing consistent differences when compared with other male's B displays. Some of these differences were so pronounced as to produce unique patterns for individual lizards.

Context

From both laboratory and field observations, the type A display was most predictably performed by males in two contexts: just after a male reached a new perch site within his territory when no other lizards were evident (assertion context), and as the first displays performed in male-male interactions. If the male-male encounter continued, type B displays were usually observed. The type B was also the most frequently seen initial display for those male-male interactions which began at close range (e.g. when the 'intruder' suddenly appeared from behind an adjoining log). Males performed both A and B displays to females. It must be noted, however, that this study was conducted during mid to late summer; no successful copulations were observed. The females may not have been sexually receptive, and their particular responses to males during this time of year undoubtedly had an effect on signals given by males to females.

Display Modifiers

As with other iguanid species, *S. u. hyacinthinus* augments its displays with various optional postures and movements (see discussion of static and dynamic modifiers in Jenssen 1977a, b; Jenssen & Hover 1976). These behavioural patterns are not always present with any one display, and their appearance can be considered as modifying the stereotyped pattern if not also its message. A variety of modifiers occurred in association with A and B displays; no modifiers appeared exclusively with one display type. The static (postural) modifiers

observed were: (1) gorged throat, (2) dewlap lowered, (3) lateral compression of the body, and (4) stiff four-legged stance.

There were two dynamic (body movement) modifiers identified. The first was the optional and varying amount of leg flexion and extension used by the lizards while bobbing. A male could vary the absolute amplitude of his displays from subtle head bobbing (low amplitude display) using only his neck muscles, to foreleg extension (moderate amplitude display), to exaggerated four legged push-ups (high amplitude display); however, within each display the relative amplitude of each bob maintained a consistent relationship with the other bobs of the display. The second kind of dynamic modifier was the variable number of bobs following the fourth bob (bobs 1-4 were always performed). These optional bobs all took on the pattern of the fifth bob.

Two of the static modifiers (dewlap lowered and lateral compression) increased in frequency of appearance as the amplitude of the displays increased. For type A, the dewlap was lowered in 3.7% of the low, 9.8% of the moderate, and 70.0% of the high amplitude displays; for type B, it was observed in 0% of the low, 25.0% of the moderate, and 87.5% of the high amplitude displays. Lateral compression in type A displays was seen during 0% of the low, 9.8% of the moderate, and 50.0% of the high amplitude displays; in type B displays it occurred in 0% of the low, 12.5% of the moderate, and 75.0% of the high amplitude displays.

Jiggling

Sceloporus u. hyacinthinus performed a third type of head bobbing pattern best described as repeated brief series of shallow rapid head bobs (Fig. 5). Each series begins with an initial bob which is longer than the rest; beyond this, however, there is not much stereotypy to the behaviour. This general kind of rapid head bobbing pattern has been observed in many species of Iguanidae. Depending upon investigator, the behaviour has received a number of

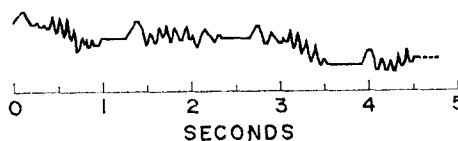


Fig. 5. A typical series of display patterns of 'jiggling' performed by a male *S. u. hyacinthinus* which was recorded at 60 frames/s.

labels such as 'jiggling' (Evans 1938; Ruibal 1967), 'shudder-bob' (Tinkle 1967); 'shuddering' (Ferguson 1970), and 'courtship nodding' (Greenberg & Noble 1944; Carpenter 1962).

Many investigators have observed jiggling being performed by males during courtship and thus have associated the appearance and function of the behaviour with the courtship context. However, jiggling by *S. u. hyacinthinus* was seen in a number of diverse contexts: (1) by solitary males patrolling their territories (often no other animal was evident) or by single 'intruders' moving through the habitat; (2) during interactions between females; (3) during interactions between males; (4) by males when approaching females; and (5) by females to males. Jiggling by *Sceloporus jarrovi* has been observed in similar contexts by Ruby (1977).

Most frequently, *S. u. hyacinthinus* performed jiggling just before and/or during locomotion. In addition, this head bobbing pattern often preceded type A and type B displays and was observed more frequently before type B than type A displays, and less frequently before both display types as the amplitude of the displays increased. For type A, jiggling preceded 11.1% of the low amplitude (subtle head movements), 9.8% of the moderate amplitude (foreleg extension), and 0% of the high amplitude (four-legged pushups) displays. For type B, jiggling preceded 32.3% of the low, 22.5% of the moderate, and 0% of the high amplitude displays.

Discussion

A functional interpretation of jiggling, for *S. u. hyacinthinus* at least, requires a retreat from the position that the behaviour is a courtship display per se. The non-heterosexual contexts in which jiggling appears and the facilitation of sex recognition by the species' sexually dimorphic colour difference make it unreasonable to restrict jiggling to courtship or instances of mistaken identity. A parsimonious interpretation of jiggling would be as a general indicator of arousal. It is not clear that jiggling has a specialized message content.

Past investigations of iguanid lizard displays have documented the characteristics of stereotypy and species-specificity for display behaviour. Studied species have generally been described as having a single unique head-bobbing pattern which is shared by the population. *Sceloporus u. hyacinthinus*, however, diverges from this concept of a limited species-typical repertoire.

We have demonstrated that *S. u. hyacinthinus* has two distinct display types (A and B). It also appears that other sceloporine lizards exhibit multiple display repertoires. Bussjaeger (1971) presented evidence indicating that *Sceloporus spinosus* and *Sceloporus horridus* have double display repertoires; both of these species are viewed as being close allies of *S. undulatus* (Bussjaeger 1971, p. 148). For *S. u. hyacinthinus*, *S. spinosus*, and *S. horridus* there is also a striking similarity in the way the second display pattern differs from the first. Within each species' repertoire the second pattern has shorter bob-plateau durations and longer inter-bob pauses than in the first pattern.

Though each species has its own distinct display patterns, all three studied sceloporine lizards may have evolved their second display pattern from the first by a similar alteration of unit durations; this suggests that some common ancestor was the progenitor of the multiple display repertoire. It would be instructive to scrutinize the display repertoires of *Sceloporus olivaceus* and *Sceloporus cautus* for the presence of the above display features since they are considered 'stem' species from the *spinosus* group to *S. undulatus* (Bussjaeger 1971, p. 148).

The second characteristic of *S. u. hyacinthinus* display behaviour which diverges from the expected is the lack of a single species-typical pattern for the type B display. The B displays demonstrated consistent differences when making inter-individual comparisons. Individual lizards having unique features to their displays have been observed in other lizards, but not at the expense of a species-typical pattern. In *Anolis nebulosus*, for example, each male performed the species' display pattern within a narrow range of durations such that some males were fast displayers and others displayed more slowly (Jensen 1971). Individually unique characteristics were also described for *Sauromalus obesus* displays which were superimposed upon a general population display pattern (Berry 1974). However, to our knowledge, *S. u. hyacinthinus* is the first reported species in which the display characteristics of some males were manifest as uniquely different display patterns, making it impossible to present a single display-action-pattern graph for the B display.

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