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# Contingency Analysis of the Agonistic Behavioral Sequence in *Sceloporus undulatus hyacinthinus*

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1987

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CONTINGENCY ANALYSIS OF THE AGONISTIC BEHAVIORAL SEQUENCE IN  
Sceloporus undulatus hyacinthinus

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CONTINGENCY ANALYSIS OF THE AGONISTIC BEHAVIORAL SEQUENCE IN  
Sceloporus undulatus hyacinthinus

A Thesis

Presented to

the Faculty of the Department of Biology  
Western Kentucky University  
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In Partial Fulfillment  
of the Requirements for the Degree  
Master of Science

by

Deborah Lynne Allison

February 1987

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I would like to dedicate this thesis to my husband, Steve, my son Joshua and my daughter Jennifer.

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37 Pages

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A contingency analysis of the sequence of actions associated with agonistic behavior of resident and introduced male Sceloporus undulatus hyacinthinus was carried out to determine the degree of stereotypy. During the time period April to June 1984 and 1985, caged pairs of adult male and juvenile female lizards were filmed on three occasions in order to gather data on resident males not involved in aggressive interactions. During the same three-month time period, a different nonresident male was introduced singly into a given resident's cage on three occasions and the interactions filmed. The films were analyzed to determine which actions were agonistic, the sequence of actions and the transition frequencies from one action to another. The sequence of actions was determined to be probabilistic, that is, the occurrence of one action influenced the probability that a specific action would follow. The most probable behavioral sequence for resident males during male-male interactions was head turn-crawl-jaw snap-lateral compression-bobbing-attack. The latter three

actions were unique to agonistic encounters. The introduced males expressed a similar behavioral sequence except that they very rarely attacked. The behavioral sequence of resident females during male-male interactions consisted of head turn-crawl-jaw snap-bobbing. Bobbing generally preceded jaw snapping in females when such male-male interactions were not taking place. The probabilistic nature of the display action pattern during agonistic behavior is similar to that observed in other iguanid lizards studied. Three levels of arousal were evident in resident males during aggressive interactions. These were 1) heightened awareness, 2) display and 3) attack. Again, this observation is consistent with those in studies carried out in other iguanid lizards.

## INTRODUCTION

Sceloporus undulatus, the fence lizard, is found in association with three major habitat types in the southern and middle United States. These include 1) woodlands or forest edges, 2) prairies or grasslands and 3) plateaus and canyons of western mountainous areas. In Kentucky, S. undulatus inhabits woodlands and forest edges (Bohlen and Wooley 1980). Many field and laboratory studies have been conducted on Sceloporus lizards (Fitch 1940, Davis 1967, Tinkel 1973), including S. undulatus subspecies (Crenshaw 1955, Kennedy 1958, Tinkle 1972a, 1972b, Vinegar 1975, Ferner 1976, Ferguson 1980). Data from those studies include growth rates, age class distributions, population replacement rates, as well as territorial, courtship and breeding activities. The annual reproductive cycle of male and female S. undulatus and environmental factors affecting this cycle have also been studied (Atland 1941, Marion 1970a, 1970b).

The subspecies common to south central Kentucky, S. undulatus hyacinthinus, emerges from hibernation in early April. Shortly thereafter, each male selects a conspicuous site on a log, fence post or rock where it will spend much of its time. From this vantage point, the male can watch for prey, potential mates and male intruders. During April males establish and maintain territories in preparation for a relatively short breeding season which begins in May and terminates by late June. Elaborate display behaviors reduce

the costs of energy expenditure and injury involved in defense of such territories from conspecifics. By advertising the level of aggressiveness through such ritualized displays, a resident male often circumvents the need for direct physical combat with a male intruder. Encounters between a resident male and a strange male can involve prolonged exchanges of threatening behavior before territorial ownership is determined. Behavior involving threats and responses to threats is called agonistic behavior. Actions associated with agonistic behavior have been studied and descriptive accounts published for a variety of iguanid lizards (Fitch 1940, Carpenter 1961, 1963, 1978, Crews 1975, Cooper 1977), including *S. undulatus* (Carpenter 1978, Rothblum and Jenssen 1978), a statistical analysis of transition frequencies between actions of an agonistic sequence has not been carried out.

Fitch (1940) and Carpenter (1978) described the actions associated with agonistic interactions between resident and intruder male *S. undulatus* in the field. At first males would exhibit laterally compressed bodies and elevated tails while maintaining a lateral orientation to one another. Additional posturing could include gular extension with movements of the head, neck and anterior trunk. During pauses in the display behavior, males would strike their opponents with their tails and hindquarters. Usually the male intruder would leave the resident's territory immediately after the latter exhibited a challenge display.

However, if the intruder remained, interactions would result in actual physical attack including chasing, biting and tail lashing. Most fights lasted for short periods of time but could continue for an hour or more. The victor chased the retreating male a short distance from the territory.

Bobbing displays associated with agonistic interactions consisted of two-legged pushups characterized by alternating extension and flexion of the front legs. Carpenter (1978) compared the bobbing display characteristics among 42 species of Sceloporus, including S. undulatus. Each had a species representative pattern. The analysis of the bobbing display pattern consisted of measuring units of movement, sequence and cadence. The bobbing display of S. undulatus consisted of a series of repeated pushups with a repeated pattern varying in cadence. The sequencing of the pattern is described in order of appearance of units of movements and the number of units performed in succession. In addition, a detailed analysis of individual differences in the male bobbing display has been carried out in S.u. hyacinthinus (Rothblum and Jenssen 1978). Those studies were conducted both in field and laboratory. They concluded that there were two types of bobbing displays: type A, wherein it served as a species recognition display and type B, wherein it served as an individual recognition display. Those two differed in the temporal patterning of the bow plateau and inter-bow pause durations. In type B, the bow plateaus are shorter in

duration and the inter-bow pauses are longer. The type A display was observed more often in resident males upon encountering a strange male. The type B bobbing display was used when the interaction between the two males continued.

Several environmental cues are known to play an important role in triggering the expression of display behavior. It is obvious that visual cues play an important role in eliciting actions associated with agonistic behavior in *S. u. hyacinthinus* as in other iguanid lizard species (Ferguson 1966, Jenssen 1970, Vinegar 1972). Other cues (e.g., olfactory) may also be important. Glands are located on various body parts of *Sceloporus* spp. Cole (1966) and Burkholder and Tanner (1974) histologically examined some of these glands and theorized about their function relating to agonistic behavior. Lizards pick up chemical cues by extruding the tongue (DeFazzio *et al.* 1977, Binsinger and Simon 1979, 1981, Gravelle 1980, Simon *et al.* 1981). Duval (1979, 1981, 1982) studied the ability of *S. occidentalis* to discriminate and use pheromones in relation to display behavior performance. These possible modes of communication need to be considered when analyzing the sequence of behavioral acts during an agonistic encounter between two male lizards.

There are many possible behavioral factors that can influence lizard display behavior. One possibility is that the preceding act can influence which act will follow. Another possibility is that the display by one lizard may

influence which display action is performed by the other lizard during the encounter. Cooper (1977) statistically analyzed agonistic behavioral sequences of male A. carolinensis to determine if there were sequential contingencies. He found the agonistic behavioral sequences to be probabilistic, that is, one action influenced the probability that a second action would follow.

In this study, display behavior of resident and introduced male S. u. hyacinthinus was videotaped and the sequence analyzed to determine the degree of stereotypy associated with agonistic behavior. Determination of which behaviors were strictly agonistic was attempted using comparisons between the behavioral sequence in male-female pairs of lizards held alone with the behavioral sequence in male-female pairs during encounters with an introduced male. In addition, a preliminary analysis of the change in body positions was also carried out. One aim of this study was to provide evidence necessary for making comparisons with the agonistic behavioral sequence of other iguanid lizards. Another aim of this study was to determine if the sequence of behavioral actions associated with aggression was predictable enough that this lizard species could be used as a model in which to study physiological factors affecting aggression.

## MATERIALS AND METHODS

Seven adult male and five juvenile female lizards were captured from rocky banks along woodland edges in the vicinity of Bowling Green, Kentucky in April 1984. Seven adult males and four juvenile females were captured from similar locations in May of 1985. All male lizards used in this study were second year or older as indicated by their snout-vent lengths, i.e.  $\geq 56$  mm, (Kennedy 1958, Tinkle 1972a, Vinegar 1975, Ferner 1976). The snout-vent lengths of males ranged between 56 mm and 76 mm with an average length of 65.8 mm. The juvenile females had snout-vent lengths that ranged from 41 mm to 52 mm with an average length of 47 mm. Snout-vent lengths for juvenile females ranged up to 62 mm (Kennedy 1958, Tinkle 1972a, Vinegar 1975, Ferner 1976).

Males to be used as residents were housed separately from one another but with a juvenile female. These pairs were established because males and females are observed to occur in pairs in the field both in and out of the breeding season (Fitch 1940, Kennedy 1958) and because other behavioral studies have used pairs (Rothblum and Jenssen 1978). Juvenile females were used in order to avoid confounding the results of agonistic encounters with courtship displays.



Each pair of lizards was housed in a wooden cage that measured 30.5 cm X 3.2 cm X 58.4 cm equipped with a sliding glass front and a screen covered opening located in the back for ventilation. Each cage contained a piece of bark, a branch with diverging twigs, water in a pebble-filled petri dish and a thermometer. Food (live fourth instar crickets, Acheta domestica) was available at all times. A 100-watt incandescent light source was placed in front of the cage at a distance that provided the appropriate temperature inside the cage. In studies carried out in other related lizard species a light-dark cycle of 14 h of light and 10 h of darkness in conjunction with a thermocycle was conducive to testicular development and reproductive behavior (Licht 1967a, 1967b, 1971). For this reason, a 14 h light and 10 h dark cycle was established using automatic timers. Engbert and Hutchison (1976) observed that S. magister preferred a higher temperature during the light phase and a lower temperature during the dark phase of the daily photoperiod. Sceloporus undulatus preferred a temperature of 33°C in association with long day lengths (Ballinger et al. 1969). Based on those studies, the cage temperature was maintained between 29°C and 31°C near the incandescent lamps during daylight hours. The temperature fell to room temperature (approximately 23°C) during the dark phase. Resident pairs were allowed one week to acclimate to these cage conditions before filming began.

Lizards were filmed from 0800 h to 1000 h in 1984 and 1300 h to 1500 h and from 1800 to 1900 h in 1985. The filming sessions occurred between the last week in April and the first week in June. The breeding season for Sceloporus species is from March to June (Fitch 1940, Atland 1941, Crenshaw 1955, Kennedy 1958, Wilhoft and Quay 1961, Marion 1970a, 1970b, Goldberg 1973, 1974). Each pair of lizards was filmed three times in the absence of a male intruder in order to determine non-aggressive behaviors. The data on agonistic interactions were obtained by introducing a strange male into a cage with an acclimated pair. In A. carolinensis, males that had fought and lost would exhibit the subordination display when challenged by the same male again. This recognition would persist up to 14 weeks (Crews 1975). Therefore, the same introduced male was not used more than once with an acclimated resident pair in this study. The film data on agonistic encounters were obtained from at least three filming sessions of each resident male-female pair immediately following the introduction of a strange male. The filming sessions of both non-agonistic and agonistic behaviors lasted for ten minutes each. If an agonistic encounter had prolonged chasing and biting (i.e., more than one minute) the session was ended prior to the end of the ten minute period.

Data from film sessions was analyzed to determine the sequence of behavioral actions and the frequency of transitions from one action to another. The sequence and

transition frequencies between actions and body positions were entered into a computer data file. From the data entered, first order contingency tables were constructed and Chi Square analysis for independence carried out. There were certain conditions the data had to meet in order for a Chi Square analysis of independence to be reliable. If for example the total repertoire of behavioral acts was ten, then a total of  $10R^2 = 1000$  observations would be required to test for significant differences from the expected frequencies, where R is the total repertoire of behavioral acts. The  $10R^2$  value has been determined to be completely adequate and  $5R^2$  values are border line. Expected transition frequencies were then calculated for transitions between each behavioral act. The  $\chi^2$  value should be valid as long as the expected values were very large. The expected values needed to be greater than one and not more than 20% could be less than five.

After establishing that significant differences existed among observed and expected transition frequencies, it was necessary to establish which transitions occurred with a greater or lesser frequency than could be accounted for by chance alone. The significance of transition frequency differences was done by calculating the Y value (Fagen and Young 1978). If  $|Y| > 0$  for a particular transition, then the preceding act directed the following act. The probabilistic sequence of actions was constructed using this statistical procedure.

## RESULTS

There were not enough observations to determine the effects of one animal's actions on the subsequent actions of another lizard. Therefore, a discussion of these interindividual interactions will not be addressed herein. There were enough observations of resident male, resident female and introduced male lizards to analyze the sequence and transition frequencies between actions for each. Data on these intraindividual non-agonistic and agonistic behavioral sequences are represented in Tables 1 through 5.

The actions and body positions that were considered for inclusion in contingency tables for Chi Square analysis of independence were as follows:

## ACTIONS:

- |                          |   |
|--------------------------|---|
| Head Turn (HT)           | - any movement of the head  |
| Crawl (CR)               | - any movement from one location to another                         |
| Bobbing (B)              | - the bobbing display was characterized by two-legged pushups       |
| Lateral Compression (LC) | - body depth increased as body width decreased                      |
| Jaw Snap (JS)            | - any rapid opening and closing of the mouth                        |
| Rapid Head Bob (RHB)     | - very rapid alternating up and down, jiggling movement of the head |
| Chasing (CH)             | - the observed lizard actively pursued the other                    |

- Attack (A) - the observed lizard actively struck the other
- Jaw Wipe (JW) - the edge of the mouth was rubbed along the substrate
- Lateral Hop (LH) - sideways movement
- Tail Movement (TM) - any pronounced movement of the tail, such as a lashing movement.

#### BODY POSITIONS:

- Body Flat (BF) - the body was completely in contact with the substrate and the legs were out to the side
- Head Up (HUF) - the head was lifted off the substrate, but the body and legs remained as in the body flat position
- Head-tail  
Up (HTU) - as with head up, except the tail was also elevated off the substrate
- Head-front legs  
Up (HFU) - head and body were elevated off the substrate by the front legs, the back legs and tail remained in contact with the substrate.

The most common non-agonistic action of resident males was head turn followed by crawling and jaw snapping (Table 1). Other behaviors such as rapid head bobs and pushups occurred at frequencies that did not allow for inclusion in the contingency matrix. It is clear that a preceding action increased the likelihood that the same action would follow. Most actions are separated in time by periods of no movement. In fact, *S. u. hyacinthinus* males spend the greatest amount of time motionless and move in sudden bursts. This strategy no doubt helps avoid predation by

Table 1. Analysis of non-aggressive behavior in resident male *S. u. hyacinthinus* during the time period April to June, 1984 and 1985. Contingency table of observed and (expected) transition frequencies among actions.

Preceding Action	Following Action			TOTAL
	Head Turn	Jaw Snap	Crawl	
Head Turn	329(305) <sup>+</sup> <sup>a</sup>	10(19) <sup>-</sup>	52(67) <sup>-</sup>	391
Jaw Snap	16 (23) <sup>-</sup>	8 (1) <sup>+</sup>	5 (5)	29
Crawl	46 (63)	6 (4)	29(14)	81
TOTAL	391	24	86	501

<sup>a</sup> The symbols represent those actions that followed a given preceding action with greater frequency than expected (+), lesser frequency than expected (-) or the same as expected (no sign) as determined by Chi Square analysis for independence and Y value determinations.

predators that respond only to moving prey. The sequence of non-agonistic actions appears to have no consistent pattern.

During aggressive encounters between resident and non-resident males, the frequency of actions observed during non-agonistic situations, such as head turn, jaw snapping and crawling increased dramatically (501 actions, Table 1 versus 1037 actions, Table 2). Of these actions, head turns lead to more head turns and jaw snapping to more jaw snapping. Crawling no longer was predictive of continued crawling, however. Instead, it was more likely to lead to jaw snapping or lateral compression. Not evident in Table 2, is the fact that once lateral compression and bobbing were expressed, the likelihood of their following crawling increased. During aggressive encounters bobbing followed lateral compression in an almost stereotyped manner. Upon lateral compression, brilliant blue patches normally concealed ventrally were exposed to the intruder. The bobbing display accentuated the newly visible pattern. The frequency of lateral compressions, bobbing displays and attacks increased dramatically compared with non-aggressive situations and were considered integral actions of the agonistic sequence. Once attacks were initiated, further attacks became very likely. Other agonistic actions associated with aggression, such as tail whipping, did not occur with sufficient frequency to be considered.

During aggressive encounters with resident males, non-resident males exhibited the same actions as the resident

Table 2. Analysis of behavior associated with aggressive encounters in resident male *S. u. hyacinthinus* during the time period April to June, 1984 and 1985. Contingency table of observed and (expected) transition frequencies among agonistic actions in resident male.

Preceding Action	Following Action						TOTAL
	Head Turn	Jaw Snap	Crawl	Lateral Compres.	Bobbing	Attack	
Head Turn	365(240) <sup>+a</sup>	32(76) <sup>-</sup>	130(129)	18(27) <sup>-</sup>	18(65)	3(30)	566
Jaw Snap	57 (77) <sup>-</sup>	58(24) <sup>+</sup>	37 (41)	9 (9)	10(21) <sup>-</sup>	11(10)	182
Crawl	72(122)	49(39) <sup>+</sup>	66 (65)	21(14) <sup>+</sup>	63(33) <sup>+</sup>	17(15)	288
Lateral Compression	2 (35) <sup>-</sup>	9(11)	21 (19)	0 (4) <sup>-</sup>	46(10) <sup>+</sup>	5 (4)	83
Bobbing	59 (60)	20(19)	35 (32)	13 (7) <sup>+</sup>	11(16) <sup>-</sup>	4 (7)	142
Attack	5 (25) <sup>-</sup>	9 (8)	11 (14)	3 (3)	3 (7)	29 (3) <sup>+</sup>	60
TOTAL	560	177	300	64	151	69	1321

<sup>a</sup> The symbols represent those actions that followed a given preceding action with greater frequency than (+), lesser frequency than (-) or the same frequency as (no sign) expected as determined by Chi Square analysis for independence and Y value determinations.



except for attack. Very few attacks were initiated by non-resident males. As with resident males, nonresident male's head turns, jaw snaps and crawling were predictive of additional head turns, jaw snaps and crawling, respectively. As with resident males, once lateral compression and bobbing displays were initiated, these actions were more likely to follow crawling than additional crawling. Again, bobbing followed lateral compression in a stereotypical manner. Lateral compression and bobbing occurred less frequency in nonresident males compared with resident males (see, Tables 2 and 3). Other agonistic actions were observed, but not with sufficient frequency to analyze statistically.

Females exhibited head turning, jaw snapping and crawling actions similar to those of males (Table 4). In addition, they exhibited a bobbing action. Unlike in males, head turning was the only action most often followed by the same action. Jaw snapping and bobbing were the most likely actions to follow crawling.

During aggressive encounters between resident and non-resident males, females made fewer head turns but more bobbing and crawling actions than during non-aggressive events (Table 5). Jaw snapping and head turns were most likely to follow jaw snapping and head turns, respectively. As during non-aggressive situations, bobbing and jaw snapping were likely to follow crawling actions.

The frequency of transitions did not increase during male-male aggressive interactions compared with transition frequencies during non-aggressive events.

Table 3. Analysis of behavior associated with aggressive encounters in non-resident male *S. u. hyacinthinus* during the time period April to June, 1984 and 1985. The contingency table of observed and (expected) transition frequencies among actions.

Preceding Action	Following Action					TOTAL
	Head Turn	Jaw Snap	Crawl	Lateral Compres.	Bobbing	
Head Turn	227(177) <sup>+a</sup>	62(83) <sup>-</sup>	95(101)	12(17) <sup>-</sup>	22(40) <sup>-</sup>	418
Jaw Snap	72 (87) <sup>-</sup>	82(41) <sup>+</sup>	33 (50) <sup>-</sup>	5 (8)	13(20) <sup>-</sup>	205
Crawl	66 (97) <sup>-</sup>	37(45)	72 (56) <sup>+</sup>	17 (9) <sup>+</sup>	37(22) <sup>+</sup>	229
Lateral Compression	4 (15) <sup>-</sup>	3 (7)	12 (9)	0 (2)	17 (3) <sup>+</sup>	36
Bobbing	49 (42)	11(19) <sup>-</sup>	27 (24)	6 (4)	5 (9) <sup>-</sup>	98
TOTAL	418	195	239	40	94	986

<sup>a</sup> The symbols represent those actions that followed a given preceding action with greater frequency than (+), lesser frequency than (-) or the same frequency as (no sign) expected as determined by Chi Square analysis for independence and Y value determinations.

Table 4. Analysis of female *S. u. hyacinthinus* behavior in the absence of male-male interactions during the time period April to June, 1984 and 1985. The contingency table of observed and (expected) transition frequencies among female actions.

Preceding Action	Following Action				TOTAL
	Head Turn	Jaw Snap	Crawl	Bobbing	
Head Turn	352(298) <sup>+a</sup>	7(24) <sup>-</sup>	66(76)	22(50) <sup>-</sup>	447
Jaw Snap	18 (26) <sup>-</sup>	6 (2)	10 (7)	4 (4)	38
Crawl	36 (80) <sup>-</sup>	16 (6) <sup>+</sup>	20(20)	47(13) <sup>+</sup>	119
Bobbing	49 (53)	7 (4)	20(13) <sup>+</sup>	3 (9) <sup>-</sup>	79
TOTAL	455	36	116	76	683

<sup>a</sup> The symbols represent those actions that followed a given preceding action with greater frequency than (+), lesser frequency than (-) or the same frequency as (no sign) expected as determined by Chi Square analysis for independence and Y value determinations.

Table 5. Analysis of female *S. u. hyacinthinus* behavior associated with male-male interactions during the time period April to June, 1984 and 1985. The contingency table of observed and (expected) transition frequencies among female actions.

Preceding Action	Following Action				TOTAL
	Head Turn	Jaw Snap	Crawl	Bobbing	
Head Turn	196(160) <sup>+a</sup>	13(24) <sup>-</sup>	77(77)	30(56) <sup>-</sup>	316
Jaw Snap	14 (23) <sup>-</sup>	13 (3) <sup>+</sup>	9(11)	9 (8)	45
Crawl	56 (81) <sup>-</sup>	20(12) <sup>+</sup>	34(39)	49(28) <sup>+</sup>	159
Bobbing	51 (54)	1 (8) <sup>-</sup>	32(26) <sup>+</sup>	22(19)	106
TOTAL	317	47	152	110	626

<sup>a</sup> The symbols represent those actions that followed a given preceding action with greater frequency than (+), lesser frequency than (-) or the same frequency as (no sign) expected as determined by Chi Square analysis for independence and Y value determinations.

Once a resident male assumes a given body position during an aggressive interaction, it is most likely to reassume that body position upon ceasing movement (Table 6). There does not appear to be a relationship between one body position and another. In a non-aggressive situation, resident males tend to spend the majority of the time in the head-front legs up position and the least amount of time lying completely flat on the substrate.

Again, the body position of resident males during aggressive interactions did not change once established (Table 7). The head-up tail-up body position was expressed infrequently during agonistic contests, but more so than during periods of no aggression. Also, the head-up feet-up body position was the one most frequently assumed by the resident male during aggressive encounters and other than head-up tail-up body position, lying flat was assumed least often. The nonresident male displayed similar body positions as the resident male. The exception was the head-tail up position. This position was not exhibited by the nonresident male (Table 8).

As with males, once a body position was assumed by females it was most frequently maintained (Table 9). Head-up feet-up was the body position most often assumed and body flat the least often assumed.

During aggressive encounters between males, there were fewer transitions between body positions observed in females (Table 10). Again, body positions once assumed were maintained. Head-up feet-up remained the most frequently

held body position and body flat the least assumed body position.

Table 6. Analysis of non-aggressive body positions in resident male *S. u. hyacinthinus* during the time period April to June, 1984 and 1985. The contingency table of observed and (expected) transition frequencies among body positions.

Preceding Position	Following Position			TOTAL
	Head-Front Legs Up	Head Up	Body Flat	
Head-Front Legs Up	310(193) <sup>+</sup> <sup>a</sup>	5(105) <sup>-</sup>	1(18) <sup>-</sup>	316
Head Up	8(109) <sup>-</sup>	167 (59) <sup>-</sup>	4(10)	179
Body Flat	3(18) <sup>-</sup>	2 (10) <sup>-</sup>	25(2) <sup>+</sup>	30
Total	321	174	30	525

<sup>a</sup> The symbols represent those body positions that followed a given preceding position with greater frequency than expected (+), lesser frequency than expected (-) or the same as expected (no sign) as determined by Chi Square analysis for independence and Y value determinations.

Table 7. Analysis of body positions in resident male *S. u. hyacinthinus* associated with aggressive encounters during the time period April to June, 1984 and 1985. The contingency table of observed and (expected) transition frequencies among body positions.

Preceding Position	Following Position				TOTAL
	Head-Front Legs Up	Head-Tail Up	Head Up	Body Flat	
Head-Front Legs Up	702(437) <sup>+a</sup>	2(15) <sup>-</sup>	18(222) <sup>-</sup>	10(58) <sup>-</sup>	732
Head-Tail Up	1 (15) <sup>-</sup>	20 (1) <sup>+</sup>	3 (8)	1 (2)	25
Head Up	28(229) <sup>-</sup>	3 (8)	348(117) <sup>+</sup>	5(31) <sup>-</sup>	384
Body Flat	10 (60) <sup>-</sup>	0 (2)	8 (31) <sup>-</sup>	83 (8) <sup>+</sup>	101
Total	741	25	377	99	1242

<sup>a</sup> The symbols represent those body positions that followed a given preceding body position with greater frequency than expected (+), lesser frequency than expected (-) or the same frequency as expected (no sign) as determined by Chi Square analysis for independence and Y value determinations.



Table 8. Analysis of body positions of non-resident male *S. u. hyacinthinus* associated with aggressive encounters during the time period April to June, 1984 and 1985. The contingency table of observed and (expected) transition frequencies among body positions.

Preceding Position	Following Position			TOTAL
	Head-Front Legs Up	Head Up	Body Flat	
Head-Front Legs Up	381(190) <sup>+a</sup>	20(175) <sup>-</sup>	8(44) <sup>-</sup>	409
Head Up	21(175) <sup>-</sup>	347(161) <sup>+</sup>	9(41) <sup>-</sup>	377
Body Flat	8 (45) <sup>-</sup>	11 (42) <sup>-</sup>	78(10) <sup>+</sup>	97
Total	410	378	95	883

<sup>a</sup> The symbols represent those body positions that followed a given preceding body position with greater frequency than expected (+), lesser frequency than expected (-) or the same frequency as expected (no sign) as determined by Chi Square analysis for independence and Y value determinations.

Table 9. Analysis of body positions of female *S. u. hyacinthinus* in the absence of male aggression during the time period April to June, 1984 and 1985. The contingency table of observed and (expected) transition frequencies among body positions.

Preceding Position	Following Position			TOTAL
	Head-Front Legs Up	Head Up	Body Flat	
Head-Front Legs Up	342(191) <sup>+a</sup>	17(107) <sup>-</sup>	8(70) <sup>-</sup>	367
Head Up	15(107) <sup>-</sup>	183 (60) <sup>+</sup>	8(39) <sup>-</sup>	206
Body Flat	10 (70) <sup>-</sup>	6 (39) <sup>-</sup>	118(25) <sup>+</sup>	134
Total	367	206	134	707

<sup>a</sup> The symbols represent those body positions that followed a given preceding body position with greater frequency than expected (+), lesser frequency than expected (-) or the same frequency as expected (no sign) as determined by Chi Square analysis for independence and Y value determinations.

Table 10. Analysis of body positions of female *S. u. hyacinthinus* associated with male-male interactions. The contingency table of observed and (expected) transition frequencies among body positions.

Preceding Position	Following Position			TOTAL
	Head-Front Legs Up	Head Up	Body Flat	
Head-Front Legs Up	277(135) <sup>+a</sup>	10(103) <sup>-</sup>	7(56) <sup>-</sup>	294
Head Up	16(107) <sup>-</sup>	207 (81) <sup>+</sup>	9(44) <sup>-</sup>	232
Body Flat	7 (58) <sup>-</sup>	11 (44) <sup>-</sup>	108(24) <sup>+</sup>	126
Total	300	228	124	652

<sup>a</sup> The symbols represent those body positions that followed a given preceding body position with greater frequency than expected (+), lesser frequency than expected (-) or the same frequency as expected (no sign) as determined by Chi Square analysis for independence and Y value determinations.

## DISCUSSION

A sequence analysis was carried out on behaviors recorded during aggressive interactions between resident and nonresident male S. u. hyacinthinus in order to determine which behaviors were agonistic and the degree of stereotypy of such behaviors. The agonistic display behavior of S. u. hyacinthinus was consistent with that described for other iguanid lizards (A. carolinensis, Crews 1975, Greenberg 1977; Dipsosaurus dorsalis, Carpenter 1961, 1963), including S. cyanogenys (Greenberg 1977). In each case, the display behavior included a lateral compression of the body and the extension of the gular region both of which increase the apparent size of the animal. Bobbing (or bowing) was an important component of the agonistic display as was lateral orientation to the opponent lizard. Many modifying signals were used such as body position and tail position. Lateral compression not only served to increase the apparent size of the signaler, but also exposed a bright blue patch otherwise hidden on the ventral surface of the body and neck. S. u. hyacinthinus males were not capable of color changes as in some other iguanids, such as A. carolinensis. Several modifying signals were identified, but could not be analyzed statistically because of their infrequent expression, with the exception of a few body positions. The behaviors described above were considered agonistic displays because they were expressed by resident males when challenged by an

introduced male and not in other contexts. An analysis to establish whether the bobbing display was type A or type B according to Rothblum's and Jenssen's (1978) criteria was not carried out. Only when the challenge-assertion displays described above failed to settle disputes, which because of cage conditions happened often, the resident male would chase and bite the intruder. These findings are entirely consistent with those of Fitch (1940) and Carpenter (1978) who studied these behaviors in field and laboratory. Thus, the behaviors expressed in caged animals in this study were considered reliably similar to those expressed in the field and statistical analyses of the behavioral sequence for degree of stereotypy was carried out.

There were 12 behavioral states identified for resident male S. u. hyacinthinus in this study (see results). Only six of these occurred frequently enough to meet criteria for statistical analysis. Of these, three were expressed in the absence of an introduced male. These were head turn, jaw snap and crawling. The frequency of their expression did go up during aggressive encounters between males. Head turns served to enhance visual scanning of the environment and male lizards would crawl to patrol their territory. Jaw snapping involved rapid gaping with an extension of the tongue. In that Sceloporine lizards have a Jacobsen's organ capable of enhancing the olfactory sensitivity over that of the nasal system (Duvall 1981), jaw snaps could serve to make the lizard more aware of its chemical surroundings. In fact, it has been shown that S. occidentalis, a closely

related western species, uses the Jacobsen's organ to detect conspecifics, possibly conspecific pheromones (Duvall 1979, 1981, 1982). Increased licking of the substrate has been observed in S. jarrovi presented with novel situations or strange conspecifics (DeFazio et al. 1977, Bissinger and Simon 1979, 1981, Gravelle and Simon 1980, Simon et al. 1981). Cole (1966) and Burkholder and Tanner (1974) have investigated several glands that have been suspected of producing such pheromones. It would seem that the sevenfold increase in the frequency of occurrence over non-aggressive observations would indicate simply an elevated state of arousal.

Lateral compression, pushup displays and attacks were characteristic only of aggressive interactions. Therefore, these display behaviors were considered to be agonistic behaviors. Lateral compression was very predictably followed by a pushup display. Lateral compression together with bobbing were most often carried out when lizards were positioned parallel to one another. The lateral compression and bobbing displays observed in this study were consistent with reports of studies carried out in other iquanid lizards (Carpenter 1961, 1963, Crews 1975), including S. cyanogenys (Greenberg 1977) and S. u. hyacinthinus (Fitch 1940, Carpenter 1978). The ventral blue patch exposed during lateral compression may enhance the signal effect of this display similar to the dewlap in other iguanid lizards. Sceloporus species do not have dewlap. Although the bobbing display is similar to that performed by other species, the

cadence and pattern of the pushups are unique to S. undulatus (Rotherblum and Jenssen 1978). This species typical display pattern seemed to occur repeatedly following a period of increased head turning and jaw snapping as if a second plateau of arousal had been reached. Duvall (1979, 1981) reported that S. occidentalis increased the frequency of this type of display after detecting chemical cues of conspecifics.

Chasing and attack were characteristic of prolonged encounters. Once attacks were initiated, they became very predictive of more attacks. In fact, once the nonresident male was removed, resident males would attack the female. Again, it appeared that attack was characteristic of a third and final plateau of arousal. The three levels of arousal correlate well with those proposed by Cooper (1977) for agonistic behavioral sequences in A. carolinensis. The three levels of arousal were 1) increased alertness 2) display and 3) attack. Furthermore, within each level actions were more ordered than would be predicted by chance. The most frequent order of actions during the increased alertness level was head turn, crawl and jaw snap. Rapid head bobs were associated with this level, as well. Lateral compression and bobbing displays were associated with the display level. Chasing and tail movements were associated with the attack level, but not very frequently. These probabilistic sequences are also in accord with findings in a similar study carried out in A. carolinensis.

The nonresident male progressed through the first two levels of arousal similar to the resident male. The sequence of behaviors in the first level was head turn, crawl and jaw snap. The frequency of jaw snapping was greater than that of the resident male. This was to be expected of a lizard in a novel environment and consistent with reports of increased substrate licking associated with transferral to novel environments from studies carried out in S. jarrovi (DeFazzio et al. 1981). Rapid head bobbing was also associated with this level of arousal in nonresident males. Nonresident males reached the second arousal level but did not display as frequently as did resident males. The third level of arousal was not reached by nonresident males. Often the nonresident male tried to escape prior to attack by the resident male.

Females did not exhibit the three levels of arousal observed in males during aggressive interactions. However, the frequency of bobbing during male-male interactions increased compared with its frequency of occurrence at other times despite the fact that the frequency of total transitions decreased during male-male interactions. Fitch (1940) removed a pair of lizards from their territory. The pair was returned to the area after several weeks. During the subsequent male-male interactions involved with re-establishment of the territory, the female hid. Under both aggressive and non-aggressive situations, crawling was most often followed by jaw snapping or bobbing. Jaw snapping appeared to be associated with chemical detection of the



environment. The fact that bobbing followed crawling and increased in frequency during male-male interactions indicated that it may function to identify sex or as an appeasement gesture. More studies of females observed in different behavioral contexts need to be conducted in order to determine the function of bobbing.

Comparisons of body positions observed during non-aggressive and aggressive situations were made in order to establish whether there were any changes in body position associated with aggressive interactions. Rothblum and Jenssen (1978) noted in *S. undulatus* that while behavioral modifiers, such as body position, were not exclusively associated with any given display, their appearance could modify the display and/or its message. The overall transition frequency of body positions during aggressive interactions was double that during non-aggressive situations in resident males. The frequency of occurrence of the head-up-tail-up position was much greater during aggressive encounters in resident males. This body position was not assumed very frequently by the introduced male. Perhaps this body position signifies heightened arousal or helps release chemical cues from proctodeal glands. Proctodeal glands have been investigated in *S. occidentalis* (Cole 1966, Burkholder and Tanner 1974) and are believed to release pheromones detectable by conspecifics. The proportion of other body position transitions were similar between aggressive and non-aggressive situations for resident males and similar to the proportions observed in

nonresident males. Therefore, without additional study, it appears that the head-up tail-up body position is associated most often with the agonistic behavioral sequence and might function to modify the agonistic display. Additional study on tail positions in various contexts is needed in order to establish its function as a display modifier.

Comparisons between the agonistic sequence among iguanid lizards should be possible despite the fact that the behavioral sequence is only mildly probabilistic overall. The levels of arousal correlate closely with those described for *A. carolinensis* (Cooper 1978). The fact that there are recognizable levels of arousal should make possible the use of *S. undulatus* as a model system in which to study the physiological mechanisms that regulate agonistic behavior. By making comparisons with other species for which there is already information, fundamental mechanisms held in common among iguanid species should be identifiable.

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