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DISPLAY VARIATION AND BEHAVIOR ASSOCIATED WITH DOMINANCE IN TWO SUBSPECIES OF *SCELOPORUS UNDULATUS* - IGUANIDAE

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DISPLAY VARIATION AND BEHAVIOR ASSOCIATED WITH DOMINANCE

IN TWO SUBSPECIES OF SCELOPORUS UNDULATUS - IGUANIDAE

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CHAPTER I

Introduction

As in most iguanid lizards, aggression in *Sceloporus undulatus garmani* Boulenger and *S. u. hyacinthinus* (Green) results in one of two forms. In natural populations males are territorial (Smith, 1946 and Hunsaker, 1962) tolerating females while in more crowded laboratory situations rigid male and weaker female social structures develop. The structure and each individual's position within it is established by the outcome of one or more agonistic encounters and maintained by further encounters and display.

The species-specific display of iguanids is a series of push-up or bobbing motions (Carpenter, 1961a, 1962a, b, 1963, 1964, and 1965; Carpenter and Grubitz, 1961; Clarke, 1965; Lynn, 1965; and Hunsaker, 1962). The value of using such stereotyped behavior patterns in phylogenetic considerations has been limited by the lack of knowledge of individual and population variations. Descriptive studies of species-specific displays of both invertebrate and vertebrate animals are numerous but few of these have involved this precise quantitative analysis (Blest, 1961).

The eight categories of Carpenter (1962a) classify, for analysis, the variations in display of iguanid lizards; those of Morris (1957a) classify the changes in coordination which may accompany its ritualization. Carpenter's categories of sequence, or number of units performed in succession, and cadence, or the measured time for the performance of each unit of movement, correspond to the categories of Morris designated as intensity change and increase or decrease in speed of performance.

In this study an attempt is made to quantify the individual, population, geographic, and subspecific variations in the display sequence and cadence of the northern prairie lizard, S. u. garmani, and the northern fence lizard, S. u. hyacinthinus. The effect of the length of sequence on the cadence of each unit is also investigated.

It has been observed that in lizards the dominant or more aggressive individual is more active (Carpenter, 1960, 1961a, b, 1962a, and 1963; Carpenter and Grubitz, 1960 and 1961; and Clarke, 1965). Carpenter (1962a) has indicated that such individuals display more frequently and tend to perform a greater number of units in each display. Evans (1936) working with Anolis carolinensis, found some correlation between weight and dominance, while in the same species, Greenberg and Noble (1942) found this correlation to be greater during breeding season. Evans (1938) found that females "gravitate" to the more dominant of two males.

Little has been done to quantify the degree such dominance affects or is affected by various behavior patterns. The present study attempts to quantify the effect of individual dominance on frequency of agonistic encounters, frequency of display, number of units per display, cadence of the display, courtship frequency, food consumption, and movement. Correlations between weight and dominance, food consumption, and cadence of the display are also noted. Sexual variations in these correlations are determined.

The effect that dominance may have upon various behaviors is important with respect to the degree to which these behaviors lend selective advantage to the individual and to the population.

CHAPTER II

METHODS AND MATERIALS

During the study data were obtained from 13 female and 16 male *Sceloporus undulatus garmani* and 5 male and 2 female *S. u. hyacinthinus* which were observed on 100 different days between June 7 and July 23 and September 18 and December 14, 1965. Individuals of the subspecies *S. u. garmani* were collected from three localities in Oklahoma: five from the area of Norman (Cleveland County), four from an area southeast of Coyle (Logan County), and twenty within a dune area south of Waynoka (Woods County). Observations were made between 0630 and 1815 hours with daily observation periods during times the animals were most active. The initial observation area, located at the University of Oklahoma Biological Station on Lake Texoma, Marshall County, was a ten by ten foot enclosure with sheet metal sides three feet high. The substrate was of sand and natural plant cover with logs, boards, cement blocks, and rocks included for additional cover and diversity. Other areas included similar enclosures both outside and indoors at the Animal Behavior Laboratory of the University of Oklahoma, Norman. Animals of both subspecies and from all locations were placed in the same enclosure. A canopy located west of the outdoor enclosures lent afternoon shade. During use of the indoor enclosure both light and heat were provided with consistent periodicity by use of a timer and Ken-rad reflector infrared heat lamps. Food consisted of laboratory (Tenebrio sp.) colonies and naturally occurring insects; water was available at all times.

Each lizard was permanently marked by toe-clipping and temporarily marked with Testor's dope. Males were given a dorsal marking of one or more colors in the pectoral region, females in the pelvic region. These color markings allow individual recognition by the observer but, as shown by Carpenter (1960), do not affect this recognition among the lizards.

Each time a display was observed, the performer and the number of units performed were recorded, and when possible, the time of one or two separate units of the display was obtained using a Clebar split-timer stop watch. The time of each unit measured was to the nearest 0.1 second. Consistent timing performance by the observer was checked by periodic measurement of a given film sequence.

The display is produced by the alternate flexion and extension of the forelegs with hind legs as a fulcrum resulting in elevation of the forebody; periods during which the forelegs are flexed and body lowered are designated as pauses. The first unit of the display was arbitrarily designated as extending from the beginning of extension of the forelegs to the second time they returned to the original position. The second unit consisted of one extension and flexion of the legs; all succeeding units were similar to the first (Figures 1, 2, and 3). The second unit differs from all others primarily in deletion of one elevation; it has been referred to as "a single" with all others being "doubles". The basic pattern of the display was obtained from analysis of movies taken at 16 or 32 frames per second.

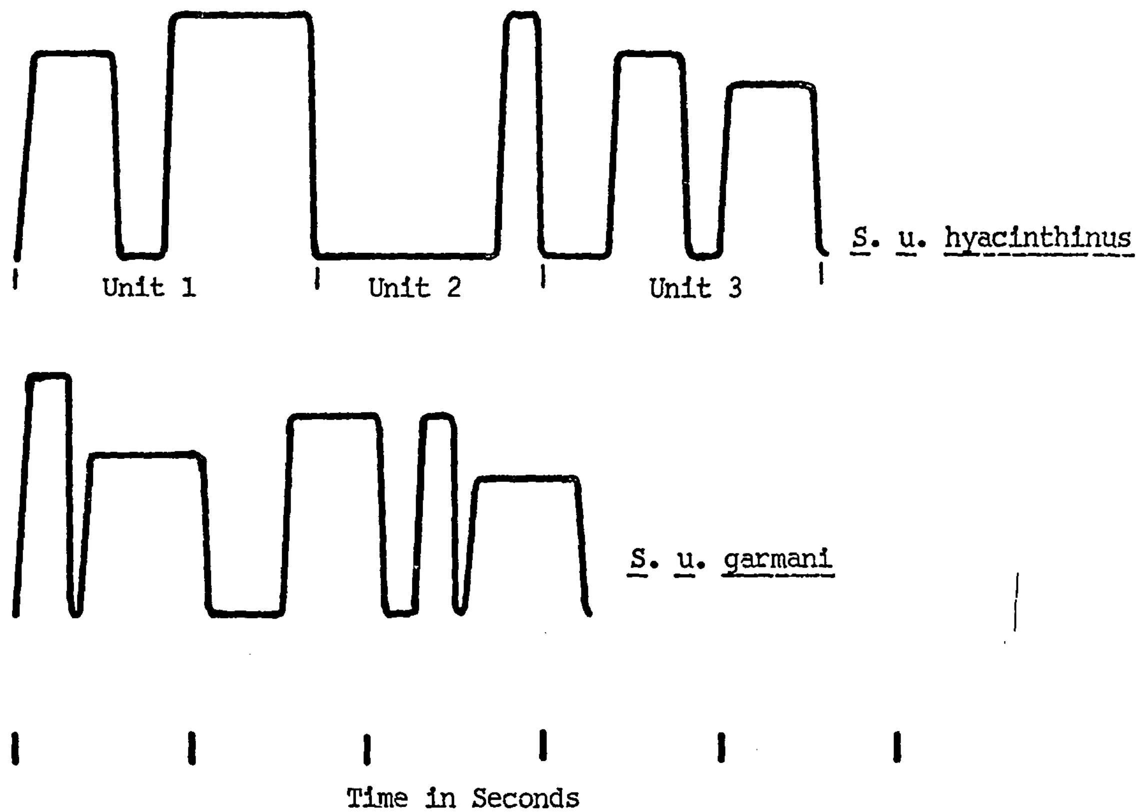

Figure 1. Generalized display-action-patterns of *Sceloporus undulatus garmani* and *S. u. hyacinthinus*.

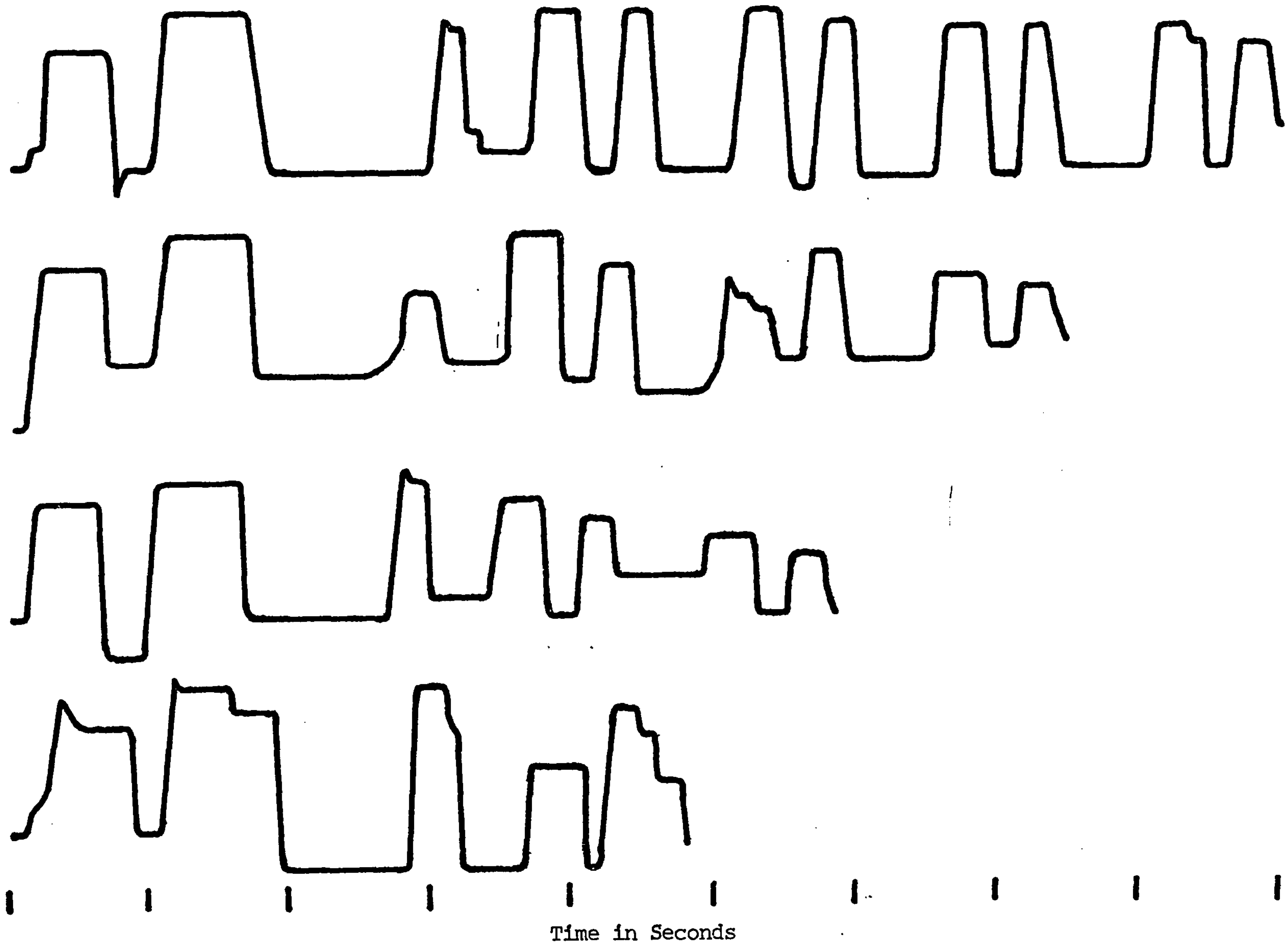

Figure 2. Display-action-patterns of a single male <u>Sceloporus undulatus hyacinthinus</u>.

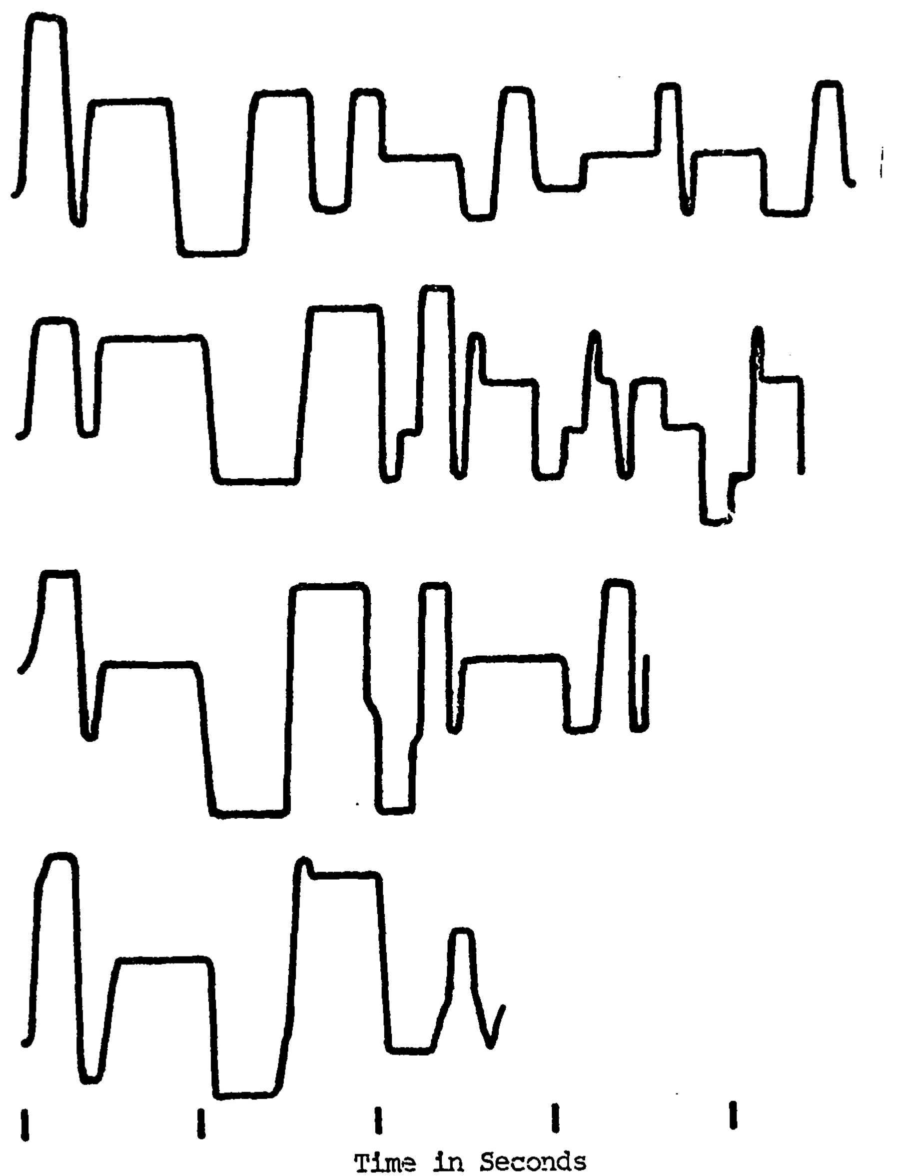

Figure 3. Display-action-patterns of four male *Sceloporus undulatus garmani*.

With the occurrence of an agonistic encounter, the dominant (winner), the subordinate (loser), and the type of behavior involved were recorded. The fraction of the encounters won was used as an index of an individual's position in the social structure.

The number of observed occurrences of courtship activity was recorded for each individual.

Note was made of the number of food items ingested by each individual.

To expedite the determination of the linear distance traveled, the enclosure was divided and marked into 25 two by two feet squares. The movements of animals within the enclosure were traced upon a similarly marked scaled map. Two individuals of the group of twenty or more were observed simultaneously during twenty minute periods. To eliminate the possible influence that members of a pair or successively observed pairs have on their activity, both the pairing of these individuals and the order in which the pairs were observed were periodically randomized. In order to eliminate diel variations in activity, observations were begun at the same hour each day and the order of observation rotated such that each pair was observed during each of the twenty minute periods of the two hour observation span. The linear distance was measured from the scaled map using a map measure.

Student's "t", nested analysis of variance, coefficients of correlation and chi square tests were used to determine the significance of variations in behavior (Snedecor, 1956).

CHAPTER III

RESULTS

The following results are based on the observation and relation of 866 agonistic encounters, 12,840 displays, 267 courtship patterns, 2280 feet of linear movement, and consumption of 1506 food items. These were observed among a total of 36 lizards, 16 male and 13 female *Sceloporus undulatus garmani* and 5 male and 2 female *S. u. hyacinthinus*.

Dominance is established as a result of the outcome of one or more agonistic encounters and is maintained by repeated encounters and by displaying. The distribution of dominance indices represents the population social structure; the index of an individual indicates that individual's position within this structure. The nearer this index is to positive unity, the more complete the individual's dominance. Figure 4 shows the distribution of dominance indices in structured male and female populations of *S. u. garmani* and illustrates certain characteristic variations. In a population of male lizards, there is normally a single individual (despot) with a dominance index near one, the remaining individuals' indices being considerably lower. Within populations of females it is more common for more than one individual to share the dominant role with subordinates having relatively higher dominance indices.

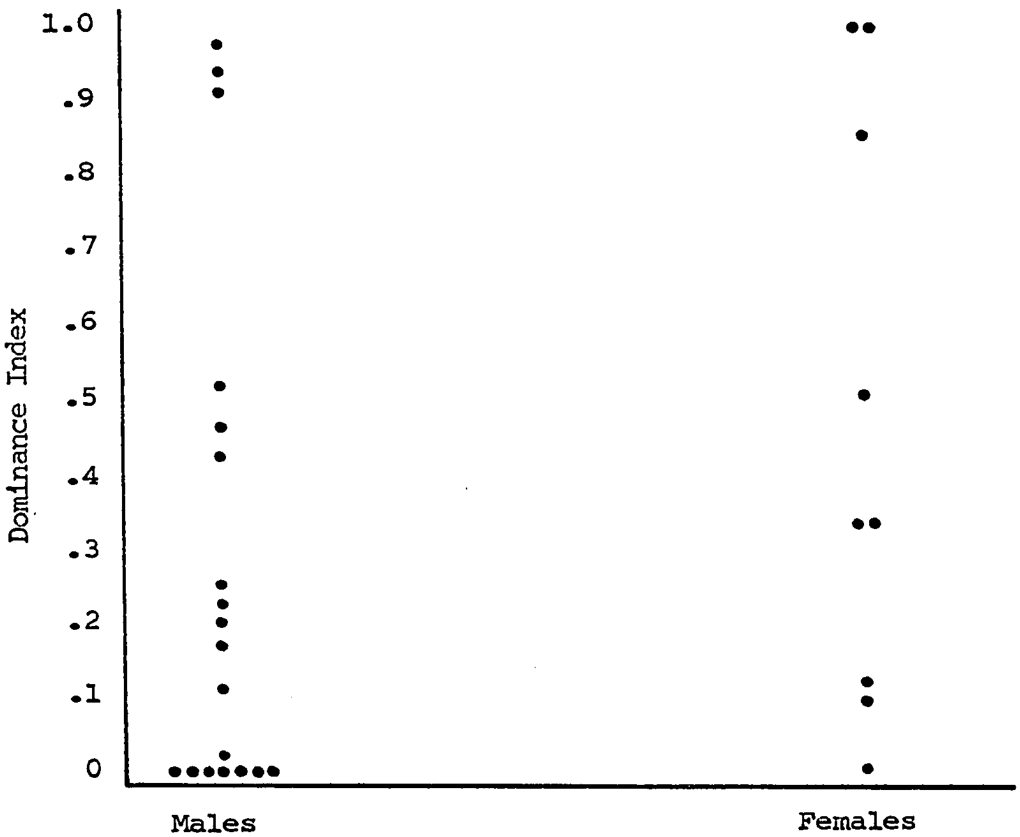

Figure 4. Distribution of dominance indices in structured male and female populations of _Sceloporus undulatus garmani_ and _S. u. hyacinthinus_.

A number of behavior patterns are related to an individual's dominance. Table 1 shows positive correlations between dominance of males and the frequency of agonistic encounters, display frequency, linear distance moved, food consumption, weight, number of units per display, and courtship participation. There is no correlation between female dominance and these behaviors. No correlation between dominance or weight and display cadence exists for either sex.

The display sequence consists of the consecutive performance of from one to fifteen units. Variation within an individual (Figure 2) and between several individuals (Figure 3) of the movement of the head through time is shown in the display-action-patterns. The average number of units performed by different individuals varies from 1.73 to 6.38; standard errors of individual performances vary from 0.028 to 0.47 units (Table 2). The differences in individual means are statistically significant; the variations in the means are not related to geographic occurrence of subspecies (Table 3). The most frequently performed number of consecutive units varies among male individuals from a series consisting of a single unit to one of five units. All females and the males collectively perform three units more frequently. The number of units performed in a given sequence does not affect the cadence of each unit ($p > 0.25$).

The average cadence of any single unit of the display is not the same for all individuals nor are all individuals equally variable (Tables 4, 5, and 6). Standard errors of cadence measurements range from 0.0032 to 0.0989 seconds for means of from 0.944 to 1.757 seconds. Females tend to be less consistent in cadence than males.

TABLE 1

CONFIDENCE LIMITS (95%) FOR CORRELATION COEFFICIENTS*

Variables	Males	Females
Number of agonistic encounters and dominance	+.45 to +.88	-.68 to +.64
Number of displays and dominance	+.36 to +.86	-.43 to +.81
Linear distance and dominance	-.08 to +.78	-.76 to +.66
Food consumption and dominance	+.22 to +.83	-.43 to +.83
Weight and dominance	+.13 to +.78	-.64 to +.64
Number of units per display and dominance	+.35 to +.86	-.83 to +.43
Courtship participation and dominance	+.55 to +.91	-.50 to +.74
Cadence and weight**		
Unit 1	-.54 to +.57	-.80 to +.58
Unit 2	-.57 to +.53	-.84 to +.50
Unit 3	-.77 to +.52	-.67 to +.90
Cadence and dominance**		
Unit 1	-.54 to +.57	-.58 to +.81
Unit 2	-.48 to +.63	-.71 to +.57
Unit 3	-.75 to +.58	-.97 to +.33

* Such confidence limits indicate that in repeated measurement of data from these bivariate populations, 5% of the correlation coefficients will be outside these limits.

** Sceloporus undulatus garmani only; all others are for both S. u. garmani and S. u. hyacinthinus.

TABLE 2

VARIATION IN NUMBER OF UNITS PER DISPLAY

Individual Code	Sex	Mode	Mean	Standard Error	Number of Measurements
Sceloporus undulatus garmani					
Y	Male	4	4.29	.103	184
Y/G	Male	3	3.37	.068	391
RBR	Male	3	2.84	.058	240
WB//	Male	1	1.73	.049	483
WGW	Male	4	4.74	.096	319
G	Male	3	2.64	.093	190
W/	Male	2	2.22	.099	457
Y/	Male	3	3.76	.028	1602
R/	Male	3	3.54	.078	607
W	Male	4	4.21	.040	1004
Bl/W	Male	2	2.01	.077	191
YRY	Female	3	2.75	.095	151
W/B	Female	3	3.62	.057	599
RWR	Female	3	3.01	.066	321
R/	Female	3	2.84	.067	204
W/	Female	3	3.15	.048	445
YWY	Female	3	2.65	.047	468
R/B	Female	3	2.85	.064	312
Y/	Female	3	2.53	.061	215
W/O	Female	3	2.47	.063	308
Population	Male	3	3.43	.017	5668
Population	Female	3	2.97	.022	3023
Sceloporus undulatus hyacinthinus					
YRY	Male	4	4.5	.47	13
R/W	Male	3	3.69	.123	180
W/R	Male	5	5.42	.231	67
B/W	Male	5	6.4	.41	39
B/W	Female	3	2.86	.226	29
Y	Female	3	2.76	.116	111
Population	Male	3	4.46	.106	299
Population	Female	3	2.78	.103	140

TABLE 3

INDIVIDUAL, GEOGRAPHIC, AND SUBSPECIFIC VARIATION IN NUMBER OF UNITS PER DISPLAY

	Degrees of Freedom	Sum of Squares	Mean Square	F	P
		Geographic			
Males					
Among locations	2	393.6	196.80	0.419	>.2500
Among individuals	8	3759.1	469.88	270.057	<.0005
Within individuals	5657	9825.7	1.74		
Females					
Among locations	2	205.8	102.90	2.481	>.1000
Among individuals	6	248.8	41.47	32.398	<.0005
Within individuals	3014	3854.9	1.28		
		Subspecific			
Males					
Among subspecies	1	302.9	302.90	1.922	>.1000
Among individuals	13	4465.7	343.52	188.745	<.0005
Within individuals	5952	10830.9	1.82		
Females					
Among subspecies	1	4.7	4.70	1.635	>.1000
Among individuals	10	454.9	50.54	39.178	<.0005
Within individuals	3152	4060.7	1.29		

TABLE 4

CADENCE OF THE FIRST UNIT OF THE DISPLAY

Individual Code	Sex	Mean in Seconds	Standard Error	Number of Measurements
		Sceloporus undulatus garmani		
Y	Male	1.149	.0075	71
Y/G	Male	1.106	.0071	102
RBR	Male	1.097	.0046	101
WB//	Male	1.191	.0038	115
WGW	Male	1.083	.0047	101
G	Male	1.005	.0041	101
OBO	Male	1.114	.0112	28
W	Male	1.169	.0065	100
Bl/W	Male	1.063	.0075	68
Y/	Male	1.050	.0070	107
R/	Male	1.085	.0060	102
W/	Male	1.081	.0060	103
Y/	Female	1.190	.0032	109
W/	Female	1.102	.0050	132
YWY	Female	1.036	.0055	104
W/O	Female	1.103	.0075	101
R/B	Female	1.102	.0070	100
YRY	Female	1.136	.0086	77
W/B	Female	1.093	.0067	108
RWR	Female	1.079	.0058	113
R/	Female	1.101	.0054	77
Population	Male	1.099	.0023	1099
Population	Female	1.104	.0024	921
		Sceloporus undulatus hyacinthinus		
R/W	Male	1.687	.0180	40
W/R	Male	1.76	.055	14
B/W	Female	1.75	.062	6
Y	Female	1.325	.0288	12
Population	Male	1.701	.0197	54
Population	Female	1.456	.0573	18

TABLE 5

CADENCE OF THE SECOND UNIT OF THE DISPLAY

Individual Code	Sex	Mean in Seconds	Standard Error	Number of Measurements
Sceloporus undulatus garmani				
Y	Male	1.015	.0071	94
Y/G	Male	1.004	.0099	114
RBR	Male	0.973	.0078	104
WB//	Male	1.218	.0043	104
WGW	Male	0.970	.0060	102
G	Male	0.993	.0076	91
OBO	Male	1.000	.0130	40
W	Male	1.168	.0100	109
Bl/W	Male	0.977	.0110	60
Y/	Male	0.982	.0066	172
R/	Male	0.946	.0088	108
W/	Male	0.944	.0088	102
Y/	Female	1.119	.0058	108
W/	Female	0.992	.0070	166
YWY	Female	1.123	.0120	116
W/O	Female	1.111	.0093	101
R/B	Female	1.033	.0084	111
YRY	Female	0.995	.0084	83
W/B	Female	1.071	.0090	106
RWR	Female	0.963	.0080	115
R/	Female	0.951	.0077	114
Population	Male	1.017	.0034	1200
Population	Female	1.037	.0035	1020
Sceloporus undulatus hyacinthinus				
YRY	Male	1.23	.099	6
R/W	Male	1.294	.0162	86
W/R	Male	1.095	.0180	22
B/W	Male	1.30	.066	6
B/W	Female	1.114	.0262	7
Y	Female	1.242	.0147	45
Population	Male	1.255	.0150	120
Population	Female	1.225	.0145	52

TABLE 6

CADENCE OF THE THIRD UNIT OF THE DISPLAY

Individual Code	Sex	Mean in Seconds	Standard Error	Number of Measurements
		Sceloporus undulatus garmani		
Y	Male	1.139	.0115	41
Y/G	Male	1.134	.0061	102
RBR	Male	1.119	.0072	47
WB//	Male	1.297	.0075	36
WGW	Male	1.053	.0054	100
W	Male	1.202	.0072	102
Y/	Male	1.073	.0073	108
R/	Male	1.046	.0059	101
W/	Female	1.061	.0103	102
YWY	Female	1.232	.0138	50
R/B	Female	1.175	.0101	48
YRY	Female	1.143	.0174	28
W/B	Female	1.151	.0075	115
RWR	Female	1.109	.0128	56
R/	Female	1.105	.0170	19
Population	Male	1.116	.0037	637
Population	Female	1.133	.0051	418
		Sceloporus undulatus hyacinthinus		
YRY	Male	1.45	.087	4
R/W	Male	1.321	.0183	52
W/R	Male	1.51	.060	15
B/W	Male	1.54	.078	8
B/W	Female	1.55	.034	6
Y	Female	1.437	.0269	30
Population	Male	1.385	.0209	79
Population	Female	1.456	.0923	36

The average cadence of male _S. u. garmani_ as measured during the summer months of June and July is not significantly different from that of fall and winter months (Table 7). The cadence of female lizards tested shows more seasonal variation.

Differences in cadence among individuals collected from a single locality are highly significant (Table 8). No significant difference in the cadence of units one and three exists among the populations from different localities. The differences in cadence of unit two among the male populations from different localities are probably significant. Although differences in the cadence of unit two of the display of females from different localities are not statistically significant, they are greater than for either unit one or three.

Comparison of the cadence of the two subspecies, _S. u. garmani_ and _S. u. hyacinthinus_, shows statistically significant variations for both sexes in units one and three, less significant variation among males for unit two and no significant difference in this unit among females (Table 9).

TABLE 7

SEASONAL COMPARISON OF CADENCE OF *SCELOPORUS UNDULATUS GARMANI*

Code	Unit		Winter	Summer	t	p
W♂	1	$\bar{y}_2$	1.169	1.175		
		s^2	0.004	0.010	0.5409	$>.50$
		n	100	105		
	2	$\bar{y}_2$	1.168	1.169		
		s^2	0.011	0.008	0.0659	$>.90$
		n	109	182		
Y♂	1	$\bar{y}_2$	1.149	1.150		
		s^2	0.004	0.003	0.0311	$>.90$
		n	71	6		
	2	$\bar{y}_2$	1.015	1.008		
		s^2	0.005	0.050	0.1615	$>.80$
		n	94	26		
YRY♀	1	$\bar{y}_2$	1.136	1.173		
		s^2	0.004	0.004	2.4084	$<.02$*
		n	77	22		
	2	$\bar{y}_2$	0.995	0.958		
		s^2	0.006	0.009	2.5595	$<.02$*
		n	83	64		
W/B♀	1	$\bar{y}_2$	1.093	1.067		
		s^2	0.005	0.028	0.3813	$>.70$
		n	108	6		
	2	$\bar{y}_2$	1.071	1.076		
		s^2	0.009	0.002	0.4705	$>.60$
		n	106	38		
RWR♀	1	$\bar{y}_2$	1.079	1.070		
		s^2	0.004	0.011	0.2577	$>.70$
		n	113	10		
	2	$\bar{y}_2$	0.963	0.950		
		s^2	0.007	0.006	0.7430	$>.40$
		n	115	26		

* Significant seasonal variation

TABLE 8

INDIVIDUAL AND GEOGRAPHIC VARIATION IN CADENCE OF *SCELOPORUS UNDULATUS GARMANI*

	Degrees of Freedom	Sum of Squares	Mean Square	F	P
First Unit					
Males					
Among locations	2	0.365	0.1825	0.9617	>.2500
Among individuals	9	2.602	0.2891	87.6061	<.0005
Within individuals	1087	3.653	0.0033		
Females					
Among locations	2	0.014	0.0070	0.9068	>.2500
Among individuals	6	1.442	0.2403	66.7500	<.0005
Within individuals	912	3.321	0.0030		
Second Unit					
Males					
Among locations	2	2.404	1.2020	5.9778	<.0250
Among individuals	9	6.189	0.6876	99.6521	<.0005
Within individuals	1188	8.294	0.0069		
Females					
Among locations	2	1.770	0.8850	2.6452	>.1000
Among individuals	6	2.042	0.3403	41.0000	<.0005
Within individuals	1011	8.398	0.0083		
Third Unit					
Males					
Among locations	2	1.443	0.7215	1.5200	>.2500
Among individuals	5	1.724	0.3448	86.2000	<.0005
Within individuals	631	2.503	0.0040		
Females					
Among locations	2	0.021	0.0105	0.1002	>.2500
Among individuals	4	1.172	0.2930	35.7317	<.0005
Within individuals	411	3.55	0.0082		

TABLE 9

SUBSPECIFIC VARIATION IN CADENCE OF SCELOPORUS UNDULATUS GARMANI AND S. U. HYACINTHINUS

	Degrees of Freedom	Sum of Squares	Mean Square	*F*	P
First Unit					
Males					
Among subspecies	1	18.930	18.930	173.1839	< .0005
Among individuals	13	3.017	0.2514	61.3170	< .0005
Within individuals	1139	4.711	0.0041		
Females					
Among subspecies	1	2.185	2.1850	35.9704	< .0005
Among individuals	10	2.236	0.2484	65.3684	< .0005
Within individuals	928	3.545	0.0038		
Second Unit					
Males					
Among subspecies	1	6.183	6.1830	9.8491	< .0100
Among individuals	14	9.300	0.6642	80.0240	< .0005
Within individuals	1304	10.804	0.0083		
Females					
Among subspecies	1	1.749	1.7490	3.2420	> .1000
Among individuals	9	11.268	1.2520	695.5555	< .0005
Within individuals	1061	1.913	0.0018		
Third Unit					
Males					
Among subspecies	1	5.066	5.0660	13.6073	< .0050
Among individuals	10	3.723	0.3723	56.4091	< .0005
Within individuals	704	4.649	0.0066		
Females					
Among subspecies	1	2.401	1.4010	9.6737	< .0500
Among individuals	5	1.241	0.2482	27.9783	< .0005
Within individuals	428	3.931	0.0092		

CHAPTER IV

DISCUSSION

Display as a mode of communication is ritualized from a previously more variable sequence of movements with the motor pattern becoming innately determined and its form species-specific (Lorenz, 1957). The reduction of variability within the pattern is necessary in establishing the motion as a communication signal (Morris, 1957b). That the display of sceloporine iguanids is sufficiently invariable to possess such signal value is shown by recognition of a model moved with the specifically correct display-action-pattern (Hunsaker, 1962). This illustrates the presence of the sensory capacity to distinguish among such displays. If the display of the iguanid lizard is to be used as a taxonomic character aiding in the determination of relationships among groups, then it is imperative that variation within the individual, among geographic intraspecific populations, among subspecies, and among species be measured and compared.

The differences in individual variations reported here for display units are substantiated particularly in males by their seasonal consistency. The lack of significant differences in intraspecific variations among geographic populations may be due to the small sample size or to the greater genetic variability generally found in populations bordering the geographic range. Two of the three populations studies, those from Cleveland and Logan counties, are such populations while that from Woods

County is centrally located.

Stein (1956), working with individual and specific differences in the "advertising song" of the Hylocichla thrushes, found consistent individual variations and specific differences associated with relative geographic ranges. Sympatric species show greater differences while allopatric species show marked similarities. Marler (1957) points out the exaggeration of this effect for signals functioning in reproductive isolation, an effect that tends to reduce the value of comparison of such signals in determining relationships above the species level.

The similarity in cadence of unit two in the display of the subspecies S. u. garmani and S. u. hyacinthinus demonstrates the similarities in signals of allopatric groups. The greater similarity in the cadence of unit two and lack of any significant difference in units one and three among geographic populations of S. u. garmani is that expected within a taxonomic unit.

Since ritualization of the signal proceeds to a more invariable form, it may be hypothesized that the lack of significant geographic variation in the first and third units is due to the stabilization of form in these phases of the display. The geographic differences in the second unit may indicate incomplete stabilization of this unit of the signal. The most significant differences in the display cadence of the two subspecies exist for the first unit, followed by the third, and second. This indicates the degree of divergence in the times of these units. The first unit has developed the largest difference and is stabilized; the third is somewhat less different and less stabilized; the second shows even less divergence and is not uniform within the populations of S. u.

garmani. Signal movements also tend to evolve to more simple form (Blest, 1961). Since the seoond unit is uniquely dissimilar and simpler in form (consists of a single elevation rather than two foreleg extensions) its ritualization of form is more advanced. The variation largely consists of the degree to which the time involved in performance of the deleted first elevation remains as a part of the portion of the unit in which the forelegs are flexed and body lowered (pause). In the second display unit of S. u. hyacinthinus, the greater portion of this time has been deleted with the entire motion.

The lack of significant geographic variation and the highly significant subspecific variation in the first unit would indicate it to be most important as a signal functioning in reproductive isolation. The greater cadence differences in males indicate that the display of the male may be of greater importance as an isolating factor than that of the female.

Under the more crowded conditions existing in experimental groups, the natural result of aggressive behavior, territoriality, is replaced by the group social structure in which the activities of the more aggressive or more dominant individuals take precedence.

The criteria determining the position of an individual within this social structure are difficult to ascertain. In lizards, although not in hens (Collias, 1943), fighting success is affected by weight. The causal factors of this relationship have been variously described. Greenberg and Noble (1942 and 1944) indicate that the greater aggressiveness is due to the greater hormone output of the larger and usually older animal. The greater correlation of weight and dominance when hormone levels are elevated during the breeding season lends support to this view (Greenberg and Noble, 1942). The posture of the fighting lizard suggests another possibility. Since lateral compression resulting in enlargement of the lateral appearance and presentation of this view to the opponent is common in agonistic encounters, some value may be attributed to the greater visible area. The larger animal ultimately presents the greater area. Lateral compression during agonistic behavior is not frequent in females; neither do females exhibit a correlation between weight and dominance.

The additional energy demands of the more active dominant male are likely responsible for the correlation between food consumption and dominance. More dominant females are neither more active nor do they consume more food.

Since no correlation exists between the cadence of the display and the dominance of the individual, it may be assumed that dominance neither affects nor is affected by it. This and the lack of correlation between cadence and weight contribute further evidence to the species-specific nature of the display.

Whether the number of units performed in a sequence affects dominance or is affected by it is uncertain. That dominance status can be altered experimentally is shown by Evans (1936b). Whether the sequence length is concomitantly altered is not known.

Hunsaker (1962) concludes that the more aggressive dominant male will acquire and defend a larger territory. The territory is defended by active patrolling; agonistic encounters between the resident and intruding males result in the retreat of the unsuccessful individual. In captivity, the unsuccessful male cannot escape, the stimulus for fighting remains, and agonistic encounters continue (Evans, 1936a). This effort by the more aggressive individual to rid the area of other males is most likely responsible for the correlation between dominance and the frequency of both agonistic encounters and display. The less territorial females (Smith, 1946) do not exhibit these correlations.

The probable correlation between the linear distance moved and dominance is attributable to the increased effort of the more aggressive individual to patrol and defend what would in nature be the territory.

Hunsaker (1962) found female sceloporines to be responsible for selection of a mate and Evans (1938) reported that Anolis carolinensis females "gravitate" to the more dominant of two males. Evans believes this to be due to the more favorable impression given the female by the more frequently displaying dominant male.

Of all behaviors compared in this study, male dominance is most closely correlated with frequency of participation in courtship. Hunsaker (1962) noted that the territorial male always interrupts the courtship of an intruding male with an aggressive challenge; this was also observed in the more dominant males of the captive group.

If, as Hansaker concludes, the more dominant aggressive male does acquire and defend a larger territory, then the probability of acquisition of a mate by this male would be increased by increasing the probability of encountering a "less territorial female." Robel (1965) has shown that more dominant prairie chickens (Tympanuchus cupido pinnatus) establish larger booming territories and are responsible for a significantly greater proportion of copulatory activity. This increase in probable mate acquisition may serve as the mechanism for selection for dominance in the male lizard.

SUMMARY

This study quantifies individual, geographic, and subspecific variations in cadence and length of sequence of the aggressive display of the iguanid lizards *Sceloporus undulatus garmani* and *S. u. hyacinthinus*. The social structure of captive populations is examined and correlations between dominance and frequency of display, movement and agonistic, courtship, and feeding behavior are quantified.

The display, a series of push-up motions of the forelegs and forebody, has a display-action-pattern of reasonably consistent form through time. The time used in performance of each unit is termed cadence, the number of units performed in succession is the length of sequence.

Variations in the mean cadence and length of sequence of the display are significantly different among individuals. No significant geographic or subspecific variations in length of sequence exist. Cadence variations of the first and third units are not significant among geographic populations of a single subspecies. This may relate either to the degree to which these phases of the signal are ritualized to stable form or to the increased genetic variability of populations bordering geographic ranges. Two of the three intraspecific populations studied were from such border localities. Significant geographic variations are found for the second unit of the display. Lack of subspecific variations in this unit further indicate its incomplete ritualization. Subspecific variations in the cadence of units one and three are

significant. The greater difference of the first unit may indicate its greater importance as a reproductive isolating mechanism. The greater geographic and subspecific variation in the display cadence of males indicates that the display of males is of greater importance in reproductive isolation than that of females.

The result of aggression in nature is territoriality; under the more crowded conditions of the laboratory, aggression results in formation of a social structure. The position of each individual is quantified as the percentage of agonistic encounters won and this dominance index used in correlation with other behavior patterns.

In males positive correlations are found between dominance and the frequency of agonistic encounters, frequency of display, linear distance moved, food consumption, weight, length of display sequence, and courtship participation. None of these are correlated with dominance in females. Cadence of the display is not correlated with dominance or weight in either sex.

The correlation of weight and dominance has been assumed by other authors to be due to the greater hormone output of the larger older animal. Another factor may play a part. Since lateral compression and orientation is a component of the display posture, the increased visual stimulus provided by the initially larger animal may be advantageous in agonistic encounters.

It may be concluded that the more dominant male would in nature acquire and defend a larger territory. In the laboratory situation the attempts of the more dominant individuals to rid, what would in nature be, the territory of other males leads to increased frequency of agonistic encounters, frequency of display, and linear movement. The energy demands of this increased activity are met by greater consumption of food.

The lack of correlation of dominance or weight with display cadence lends additional evidence to the species-specific nature of the display.

Dominance is most strongly correlated with frequency of participation in courtship. In the captive situation the more dominant male will frequently interrupt the courtship pattern of other males. In nature the larger territory of the more aggressive male probably increases the chance of acquiring a mate. This increase in probable mate acquisition may serve as the mechanism of selection for dominance in the male lizard.

LITERATURE CITED

Blest, A. D. 1961. The concept of ritualization, p. 590-606. In W. H. Thorpe and O. L. Zangwill, ed., Current problems in animal behaviour. Cambridge Univ. Press, Cambridge.

Carpenter, C. C. 1960. Aggressive behaviour and social dominance in the six-lined racerunner (Cnemidophorus sexlineatus). Animal Behaviour 8: 61-66.

______. 1961a. Patterns of social behavior in the desert iguana, Dipsosaurus dorsalis. Copeia 1961: 396-405.

______. 1961b. Patterns of social behavior of Merriam's canyon lizard (Sceloporus m. merriami - Iguanidae). Southwestern Naturalist 6: 138-148.

______. 1962a. Patterns of behavior in two Oklahoma lizards. Am. Midland Naturalist 67: 132-151.

______. 1962b. A comparison of the patterns of display of Urosaurus, Uta, and Streptosaurus. Herpetologica 18: 145-152.

______. 1963. Patterns of behavior in three forms of the fringe-toed lizards (Uma - Iguanidae). Copeia 1963: 406-412.

______. 1964. Comparative behavior of the lava lizards (Tropidurus) of the Galapagos Islands. (Abstr.) Am. Zoologist 4: 274.

______. 1965. The display of the Cocos Island Anole. Herpetologica 21: 256-260.

Carpenter, C. C. and G. Grubits, III. [sic] . 1960. Dominance shifts in the tree lizard (Urosaurus ornatus - Iguanidae). Southwestern Naturalist 5: 123-128.

Carpenter, C. C. and G. Grubitz, III. 1961. Time-motion study of a lizard. Ecology 42: 199-200.

Clarke, R. F. 1965. An ethological study of the iguanid lizard genera Callisaurus, Cophosaurus, and Holbrookia. The Emporia State Research Studies 8 (4): 1-66.

Collias, N. E. 1943. Statistical analysis of factors which make for success in initial encounters between hens. Am. Naturalist 77: 519-538.

Evans, L. T. 1936a. A study of a social heirarchy in the lizard, Anolis carolinensis. J. Genet. Psychol. 48: 88-111.

______. 1936b. Behavior of castrated lizards. J. Genet. Psychol. 48: 217-221.

______. 1938. Courtship behavior and sexual selection of Anolis. J. Comp. Psychol. 26: 475-498.

Greenberg, B. and G. K. Noble. 1942. Dominance, social order and territory in the lizard, (Anolis carolinensis). (Abstr.) Anat. Record 84: 508.

______. 1944. Social behavior of the American Chameleon (Anolis carolinensis Voight). Physiol. Zool. 17: 392-439.

Hunsaker, D., II. 1962. Ethological isolating mechanisms in the Sceloporus torquatus group of lizards. Evolution 16: 62-74.

Lorenz, K. 1957. The past twelve years in the comparative study of behavior, p. 288-310. In C. H. Schiller, ed., Instinctive behavior. Intern. Univ. Press, New York.

Lynn, R. T. 1965. A comparative study of display behavior in Phrynosoma (Iguanidae). Southwestern Naturalist 10: 25-30.

Marler, P. 1957. Specific distinctiveness in the communication signals of birds. Behaviour 11: 13-39.

Morris, D. 1957a. The reproductive behaviour of the Bronze Mannikin (Lonchura cuculiata). Behaviour 11: 156-201.

______. 1957b. 'Typical intensity' and its relationship to the problem of ritualization. Behaviour 11: 1-13.

Robel, R. J. 1965. Function of territory size in mating success of booming Tympanachus [sic] cupido pinnatus. (Abstr.) Bull. Ecol. Soc. Am. 46: 175.

Smith, H. M. 1946. Handbook of lizards. Comstock Publ. Co., Ithaca. 557 p.

Snedecor, G. W. 1956. Statistical methods. 5th ed. Iowa State Univ. Press, Ames, Iowa. 533 p.

Stein, R. C. 1956. A comparative study of 'advertising song' in the Hylocichla thrushes. Auk 73: 503-512.