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PHYLOGENETIC SIGNIFICANCE OF THE COMPARATIVE ETHOLOGY OF THE SPINOSUS GROUP OF SCELOPORUS (IGUANIDAE)

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PHYLOGENETIC SIGNIFICANCE OF THE COMPARATIVE ETHOLOGY OF THE <u>SPINOSUS</u> GROUP OF <u>SCELOPORUS</u> (IGUANIDAE)

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This section is the last to be written and the first to be read. I hope that those whom I acknowledge feel that it really need not be written. To let those who did not share this task with me know who helped me complete this study, I would like to acknowledge gratefully the assistance of these people.

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CHAPTER I

INTRODUCTION

The study of lizard behavior as separate from lizard life history was not initiated until G. K. Noble and colleagues studied the stereotyped courtship behavior of iguanids in the 1930's (Noble and Teal, 1930; Noble and Bradley, 1933). Few other studies were done on lizard behavior until the 1960's when Carpenter (Carpenter and Grubitz, 1961) and Hunsaker (1962) independently concluded that the push-up or head-bobbing movements for certain iguanids were stereotyped, "species-specific" displays. They considered the displays to be functional analogues of territorial bird songs.

Hunsaker (1962) determined species-specific displays of the *torquatus* group of *Sceloporus* and performed experiments which showed that the displays possibly functioned as an isolating mechanism. Although his conclusions were probably correct, recent data have shown his proofs, especially his female choice discrimination tests, to be questionable (Carpenter, pers. comm.). In this test, Hunsaker presented females of the *torquatus* group of lizards with a choice of bobbing models, one performing the species display, the other a "nonsense" display. The females chose the species display more often. However, his species-specific displays were incomplete and he apparently presented the displays at the wrong cadence (Jenssen, 1969). Jenssen (1969) performed a similar experiment in which he tested the ability of females of Anolis nebulosus to discriminate between film loops of males performing normal or altered displays. A majority of the females showed a preference for the normal display. Jenssen's data suggested that the display functioned as an isolating mechanism and that females acted as a selective factor to stabilize a display pattern in a population.

Since 1961, Carpenter and his students have been active in studying many aspects of lizard behavior and in determining the display-action-patterns of many iguanids and certain Agamidae (the old world counterpart of Iguanidae which perform similar displays). In addition to the previously mentioned studies, Carpenter and his students have studied the following genera: the sand lizards, Uma, Holbrookia, Cophosaurus and Callisaurus (Carpenter, 1963, 1967a; and Clarke, 1965); the horned lizards, Phrynosoma (Lynn, 1965), fence lizards, Sceloporus (Carpenter, 1961a, 1962a; and Bussjaeger, 1967); Uta, Urosaurus and Streptosaurus (Carpenter, 1962b); Dipsosaurus (Carpenter, 1961b); Tropidurus (Carpenter, 1966a); Amblyrhynchus (Carpenter, 1966b); Conolophus (Carpenter, 1969) and Anolis (Carpenter, 1965). Other investigators have studied the Anolis roquet group (Gorman, 1968 and Ruibal, 1967) and Uta (Ferguson, 1969 and McKinney, 1967). Except for the study by Ruibal, all showed each species to have a distinct "species-specific" display. Carpenter (1962b, 1963, 1966a), Clarke (1965), Lynn (1965), Bussjaeger (1967) and Gorman (1968) have utilized display-action-patterns and behavior as a tool to help clarify the taxonomic problems or to help interpret proposed phylogenies.

Others have been concerned with variation within the display. Yoshida (1966) investigated ontogenetical variation and development of the display. Griffith (1966) and Taylor (1965) investigated sub-specific variations in the displays of *Sceloporus undulatus*. Bussjaeger (1967) showed that the amount of display variation depended upon the species within the *spinosus* group. Jenssen (1969) statistically analyzed both the variation present within one population of *Anolis nebulosus* and the variation in the displays due to age. Ferguson (1969) determined the geographic variation in the display-action-patterns of various populations of *Uta*.

These studies have shown that the term "species-specific display" can not be interpreted to mean that a species has only one display-action-pattern. Displays performed by some species may contain many variations or slightly different patterns, all of which are unique for that species. Present data agree with this definition. One qualification is that allopatric species of lizards may have similar displays; Bussjaeger (unpublished) found the displays of *S. undulatus hyacinthinus* and *S. occidentalis* to be very similar. No sympatric lizards have been found with identical display-action-patterns. The only sympatric species known to have similar displays are *S. occidentalis* and *S. graciosus*, but their cadences and thus the temporal patterns of their displays are distinct

(Marcellini, 1966).

Relationships of the Spinosus Group of Sceloporus

Over 120 species and subspecies are recognized in the lizard genus Sceloporus. The genus is typical of North American iguanids in possessing femoral pores. Characters which distinguish it from other iguanid genera are: the presence of a depressed body, imbricate and keeled dorsal scales, enlarged occipital shield, keeled digital lamellae and distinct tympana and the absence of abdominal ribs, collar, gular pouch, pterygoid teeth and dorsal crest. Being a recently evolved and plastic genus, Sceloporus presents a great diversity in size, coloration and habitat preference. This makes the group very interesting from the standpoint of species formation and geographic distribution (Smith, 1939).

In his monograph on the Mexican and Central American forms of Sceloporus, Smith (1939) divided the genus into 15 species groups. For each form, he summarized the available information that related to their description, distribution and habitat preference. He also presented his concept of the evolutionary history of the genus, postulating relationships between and within the species groups (Figures 1 and 2).

The group under study, the spinosus group of Sceloporus, was originally defined by Smith as containing 11 species and 21 forms, ranging from southwestern United States to Guatemala. He characterized the group as follows:

> The characters held in common by members of this group are: absence of a dorsal, light-bordered nuchal collar; dorsal scales relatively large

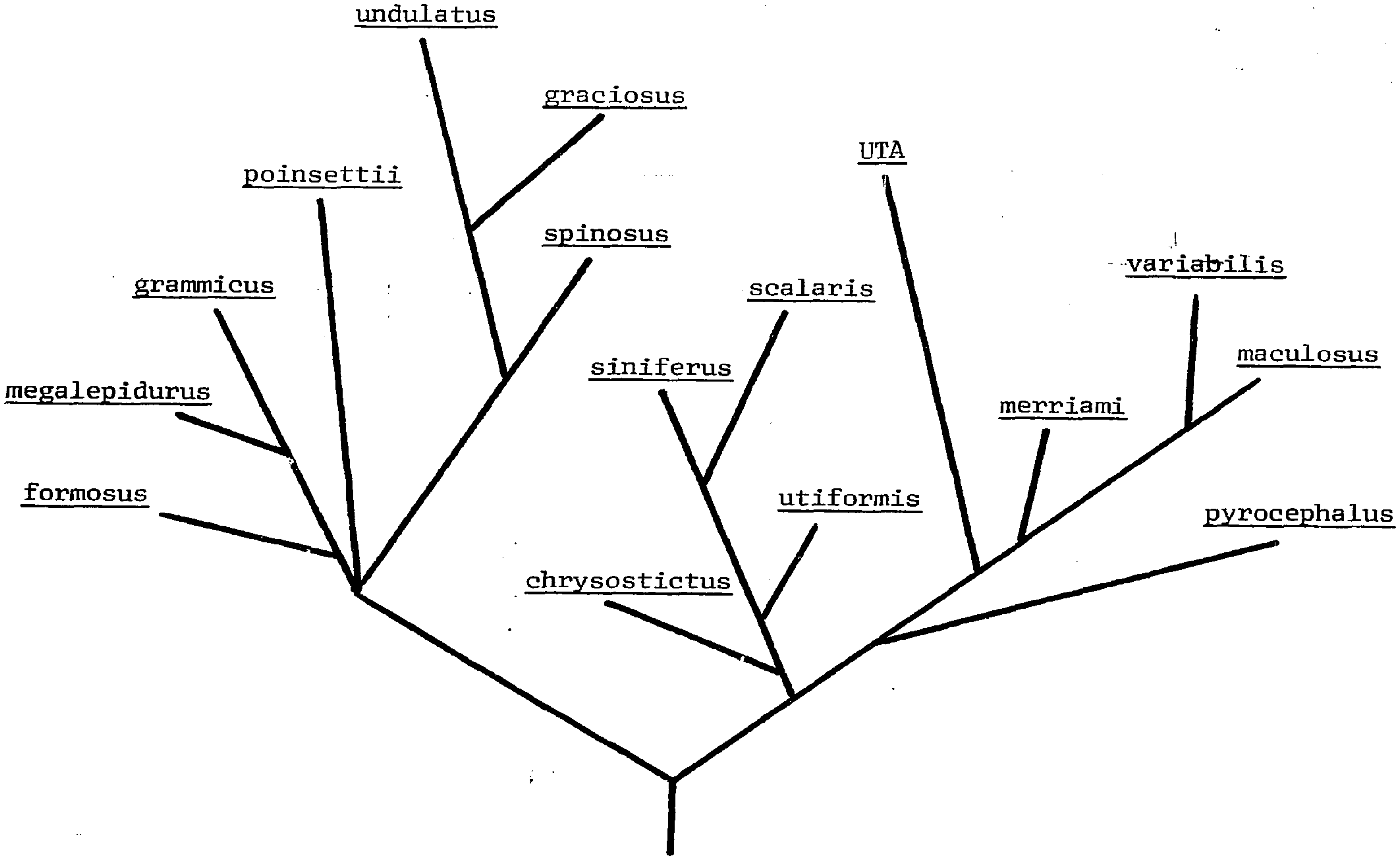

Figure 1. Phylogenetic relationships of the species groups of <u>Sceloporus</u>. (After Smith, 1939).

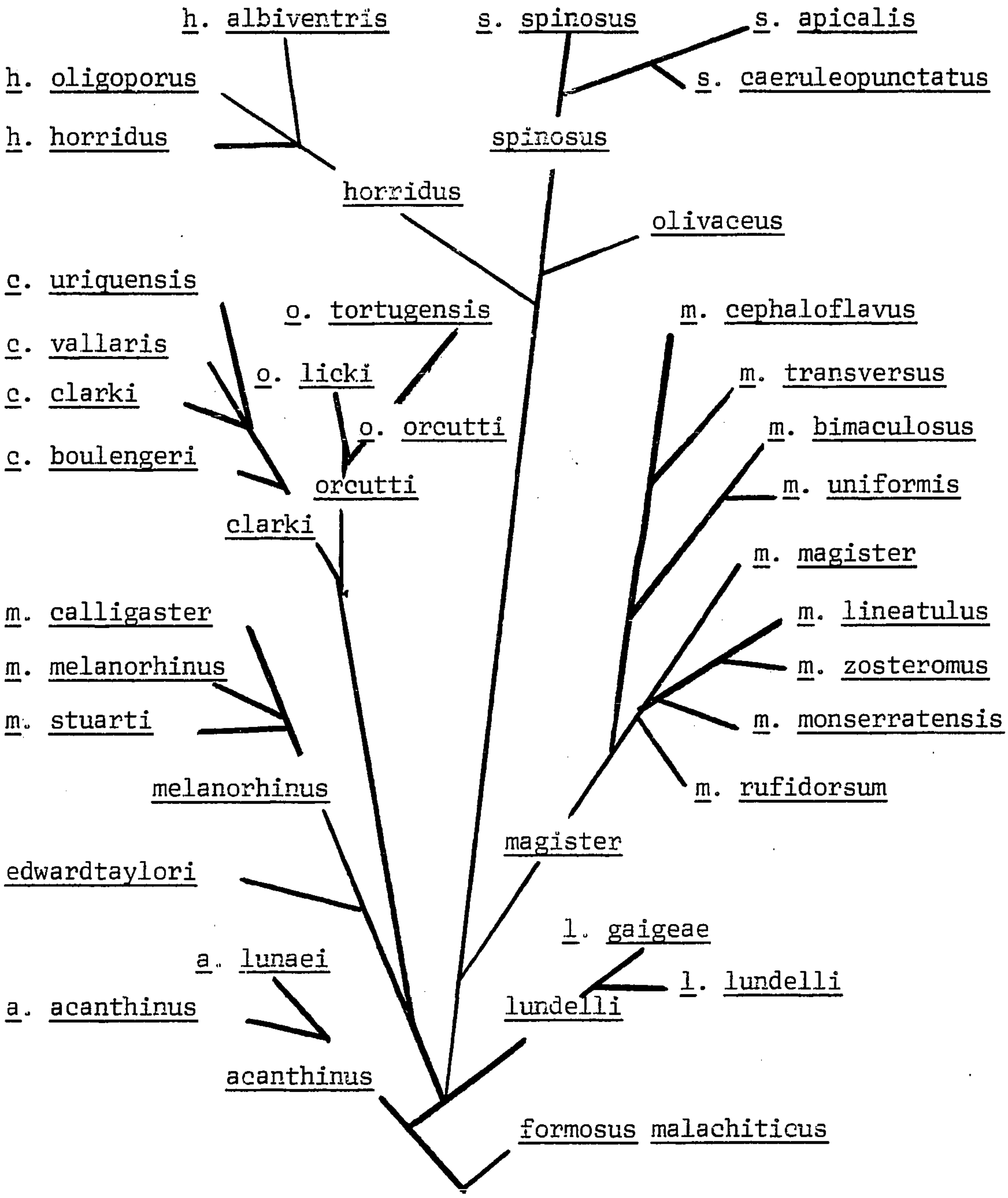

Figure 2. Phylogenetic relationships of the forms in the spinosus group of Sceloporus as modified from Smith (1939) to include recently described forms.

> (minimum, 26; maximum, 40); dorsal scales strongly mucronate (except _o. orcutti_); ventral scales smooth, notched; post-anals enlarged in males; scales on posterior surface of thigh large; supraoculars in a single series, usually very large, usually partially in contact with median head scales; femoral pores widely separated medially; dorsal surface not a brilliant blue in males (except _lunaei_ and _acanthinus_); belly colored in males (except _h. albiventris_ and _edwardtaylori_); relatively a large size (maximum snout-vent measurement of smallest species, 86 mm.; of largest species, 140 mm.).

The primary basis of Smith's phylogenetic concept of the _spinosus_ group is based on dorsal color pattern, gross morphology and zoogeography. Of the two main divisions, one line (_magister_) is characterized by brownish coloration with dorsolateral stripes or a broad dorsal band; the other line (_clarki_) is represented by a uniform "plain" nonpatterned grayish back. Apparently, Smith (1939) believes that the _spinosus_ group originated from Guatemalan ancestral forms (near _acanthinus_). Then, the group underwent secondary radiation with the madro-tertiary geoflora into a central highland form (_magister_) and a tropical western coastal form (_clarki_). The latter's ancestor gave rise to _melanorhinus_, _edwardtaylori_, and _orcutti_. The highland form radiated into _spinosus_, _horridus_ and _olivaceus_, with _horridus_ secondarily invading the western coast.

Except for the recognition of new subspecies and the deletion of two species, the _spinosus_ group of _Sceloporus_ is the same as Smith defined it. In 1942, Smith re-defined the _formosus_ group to include the lizards known as _acanthinus_ and _lunaei_ and renamed the former _malachiticus acanthinus_. I agree that they belong to this group and accept Smith's (1942) conclusion that they represent the connecting forms to the spinosus group. However, Stuart (1963) considers both as subspecies of acanthinus and distinct from malachiticus. As of March, 1969, both authors (pers. comm.) were still convinced that their respective positions were correct. Since their conclusions were based on different interpretations of the same material, the taxonomy of these forms is questionable. However, since Stuart has been more active in collecting Guatemalan forms and Peters and Donoso-Barros (1970) recognizes Stuart's revision, I will refer to them as a. acanthinus and a. lunaei.

The only other taxonomic changes since Smith (1939) have been the recognition of the following subspecies: magister bimaculosus, m. transversus, m. uniformis by Phelan and Brattstrom (1955); m. cephaloflavus by Tanner (1956); clarki vallaris by Shannon and Urbano (1954); c. uriquensis by Tanner and Robison (1959); melanorhinus stuarti by Smith (1948), and spinosus apicalis by Smith and Smith (1951). However, Banta (1961) in an unpublished dissertation indicated that two of the taxa of Phelan and Brattstrom were synonyms; he stated m. magister was synonomous with m. uniformis and m. bimaculosus. Since Banta has not published this revision, the previous subspecies nomenclature of magister is valid.

Aside from these taxonomic changes, the only other published information on the Mexican forms of the spinosus group have been ecological notes or distributional records.

Several of the U. S. forms of the spinosus group have been extensively studied. *Sceloporus olivaceus*, the rusty lizard, was the subject of a five year population study by Blair (1960). This was preceded by an ethoecological study of the same lizard by Newman and Patterson (1909). The granite spiny lizard, *o. orcutti*, has been the subject of extensive investigation by Mayhew on its biology (1963a), reproduction (1963b), and temperature regulation (1963c). Recently, his student, Weintraub, studied the winter behavior (1968), size relationships (1969) and homing behavior (1970) of this species. As yet, there have been no extensive studies published on *clarki* or *magister* except for their inclusion in studies on thermoregulation (Bogert, 1949), integument reflectance (Aslatt, 1939), oxygen consumption (Dawson and Poulson, 1962), and brief ecological notes.

In addition to ascertaining the relationships within the *spinosus* group, closely related members of other species groups were studied, as available, to determine their relationship to the *spinosus* group. *Sceloporus cautus* of the *undulatus* group was examined; Smith (1939) hypothesized it to be the connecting form to the *spinosus* group (Fig. 1). However, William P. Hall III (pers. comm.) believes *cautus* is actually another population of *olivaceus* (*spinosus* group). He reached this conclusion on the basis of karyotypes and other characteristics of a population found connecting these two formerly allopatric species. The morphological similarity between these groups is further emphasized by the fact that in southern Texas, it is exceedingly difficult to separate young *olivaceus* from *undulatus*.

Some members of the formosus group of *Sceloporus*, *a*. *acanthinus*, *a*. *lunaei* and *asper*, were observed. The most prominent difference of this species group from the *spinosus* group is that the *formosus* group's basic coloration is greenish or olive-green; otherwise, except for minor head scutellation differences, it is very similar to the *spinosus* group. It was hoped that behavioral data on these forms would allow some interpretations on the status and relationships of the *spinosus*, *formosus* and *undulatus* groups.

Validity of Behavioral Studies

Comparative studies of species-specific displays have been few, and many questions remain to be solved, as to the importance of this characteristic in systematics. At what taxon level or levels are these stereotyped displays most useful? How useful are the displays in indicating phylogenetic relationships? Alexander (1969) states that behavior is a characteristic more useful at the alpha-level of taxonomy--species characters such as those used to identify sibling species--than at the beta-level which functions to indicate phylogenetic relationships. Nevertheless, this is not an absolute rule and despite the fallacies mentioned by Marler (1957) in using behavioral isolating mechanisms as phylogenetic characters, they have been used to indicate phylogenetic relationships. The courtship calls of crickets (Alexander, 1957) and anurans (Blair, 1962; Littlejohn, 1959) have been used to indicate relationships, but they have emphasized that conclusions drawn from behavior must be supported by other lines of evidence (Littlejohn, 1969).

The usefulness of behavior in lizard systematics is at the same stage as reported for the above vertebrate groups. This is indicated by the opposing views of two discussants of Carpenter's paper presented at a 1965 Lizard Ecology Symposium. In discussing the value of the display-action-patterns, Dr. Tinkle was quoted, "It is very unlikely that these behavior patterns will ever be extremely useful in phylogeny." Dr. W. F. Blair stated an opposing view: "It seems to me that the different display patterns probably serve the same function for the lizards that the different calls serve for the toads." It clearly follows since anuran mating calls have phylogenetic significance, that Blair felt lizard display-action-patterns may show similar relationships (Carpenter, 1967b).

Within the last decade, studies of lizard behavior have clarified the specific and generic status of iguanid lizards and their relationships (Clarke, 1965; Carpenter, 1962b, 1963, 1967a; Bussjaeger, 1967; and Gorman, 1969). Some behavioral studies were unable to supply the critical data. For example, _Uma_ _ornata_ and _Uma_ _inornata_ which could not be separated on behavioral differences (Carpenter, 1963) have been shown to be reproductively isolated (Mayhew, 1964). Also, Ruibal (1967) was unable to correlate behavioral data with the inter-island relationships of 8 of 12 West Indian species of _Anolis_. However, he only studied a particular behavioral reaction, the initial response, which would be extremely limiting in elucidating relationships. Behavior is another characteristic of the animal. It is a trait to be used just as the more standard morphological characters, scale counts, or coloration are used to determine either the status of a species or the relationships of a group of animals. Likewise, behavioral data have the same fallacies as these other characters.

The primary aim of this study was to determine display-action-patterns of the *spinosus* group of the genus *Sceloporus*. In addition, I hoped to determine the systematic value of these behavior patterns and to ascertain if, combined with other behavioral evidence and karyotype data, they could be useful in interpreting and postulating the phylogeny of the species within the *spinosus* group of *Sceloporus*.

CHAPTER II

METHODS AND MATERIALS

This study of the mainland Mexican and Central American forms of the *spinosus* group of *Sceloporus* was done primarily at the Animal Behavior Laboratory, University of Oklahoma, Norman, Oklahoma, between April, 1966 and July, 1969. Two months, June and July 1966, were spent observing some forms at the University of Oklahoma Biological Station near Willis, Oklahoma. In addition, 78 days were spent on six field trips to Mexico (five) and Guatemala (one) to obtain lizards used in this study. Besides obtaining lizards, the field trips permitted the collection of pertinent ecological data and exact locality data which was necessary for meaningful interpretations of display variations. All species of the *spinosus* group and the most closely related forms of two other groups were represented. Table 1 summarizes the forms available for study and numbers of each utilized in analyzing their displays. Previously studied forms of the spinosus group are listed separately as they were primarily used to ascertain interspecific social relationships because their display behavior had already been described (Bussjaeger, 1967).

Table 21 (Appendix I) presents the following data for each individual collected for this study: taxa; sex; identification

Table 1. A summary of species, number of individuals available, number of individuals photographed, and total number of displays used in determining display-action-patterns.

Species of *Sceloporus*	Number of Lizards	Number of individuals photographed	Total Number of displays analyzed
spinosus group			
melanorhinus calligaster	26	14	151
m. stuarti	1	0	0
s. spinosus	23	8	44
s. caeruleopunctatus	22	10	85
s. apicalis	8	3	15
h. horridus	23	5	28
h. oligoporus	27	17	158
h. albiventris	22	10	59
lundelli gaigei	1	1	4
edwardtaylori	24	9	42
	177	77	586
formosus group			
a. acanthinus	8	3	7
a. lunaei	11	8	59
asper	4	3	25
	23	14	91
undulatus group			
cautus	2	2	18
spinosus group of M.S. thesis*			
olivaceus	35		
magister	9		
c. clarki	6		
c. boulengeri	7		
	57		

*Displays determined by Bussjaeger, 1967 marks; initial snout-vent length, total length and body weight; and collection locality. Table 22.(Appendix II) lists the collection localities while Figures 3 and 4 indicates their location on a map of Mexico. In addition, 16 lizards were obtained by friends. Also, hatchlings of 10 clutches of eggs of various species were observed.

During the study, the lizards were housed in either large enclosures (indoor, 3.3 x 5 m; outdoor, 5 x 5 m) constructed of sheet metal sides, or terraria ranging in size to 1.3 x 1.3 m. In all cases, sand formed the substrate; retreats and raised areas were provided by concrete blocks, rocks, stumps and branches. In the outdoor enclosures, some vegetation was left to provide additional cover. During the summer, the lizards were fed insects and small arthropods obtained by sweeping weedy pastures. During the winter, the lizards were fed commercially purchased grey crickets (Gryllus) and mealworms (Tenebrio larvae). Also in winter, heat and sun lamps were used to provide warmth and to supplement sunlight.

The lizards were marked permanently by a toe clipping system. They were painted dorsally with a coded series of Testor's butyrate dope so that sex, species and individuals could be readily identified. The lizards were repainted as required. In many cases, color patterns, tail length or other unique features of an individual were used to supplement the color code.

Observations on the lizards' social interactions were concentrated in four different observation periods: June, 1966;

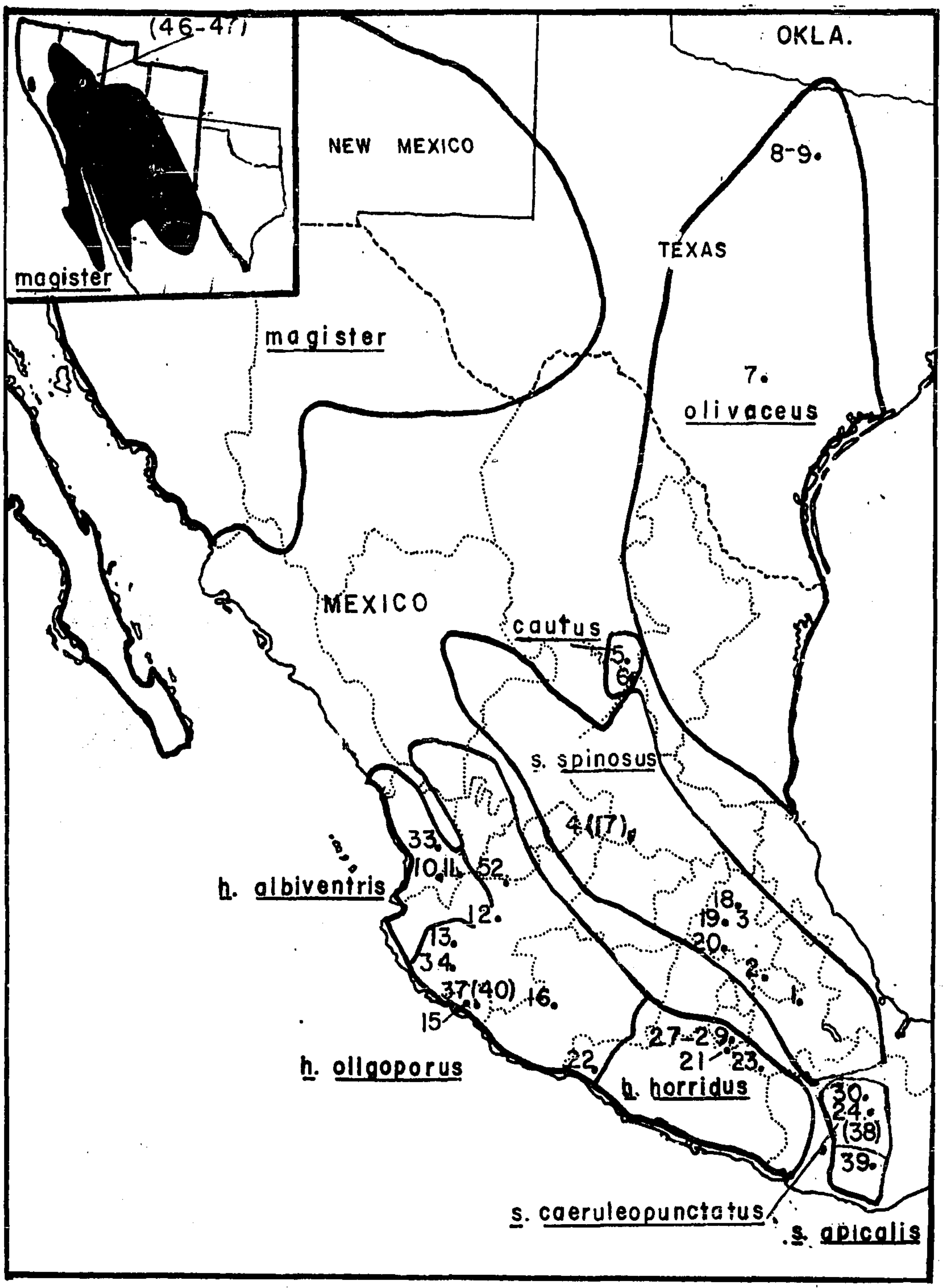

Fig. 3. Collection localities and distribution of the species of the spinosus group with dorsolateral stripes (magister, olivaceus, spinosus and horridus) and cautus of the undulatus group of Sceloporus.

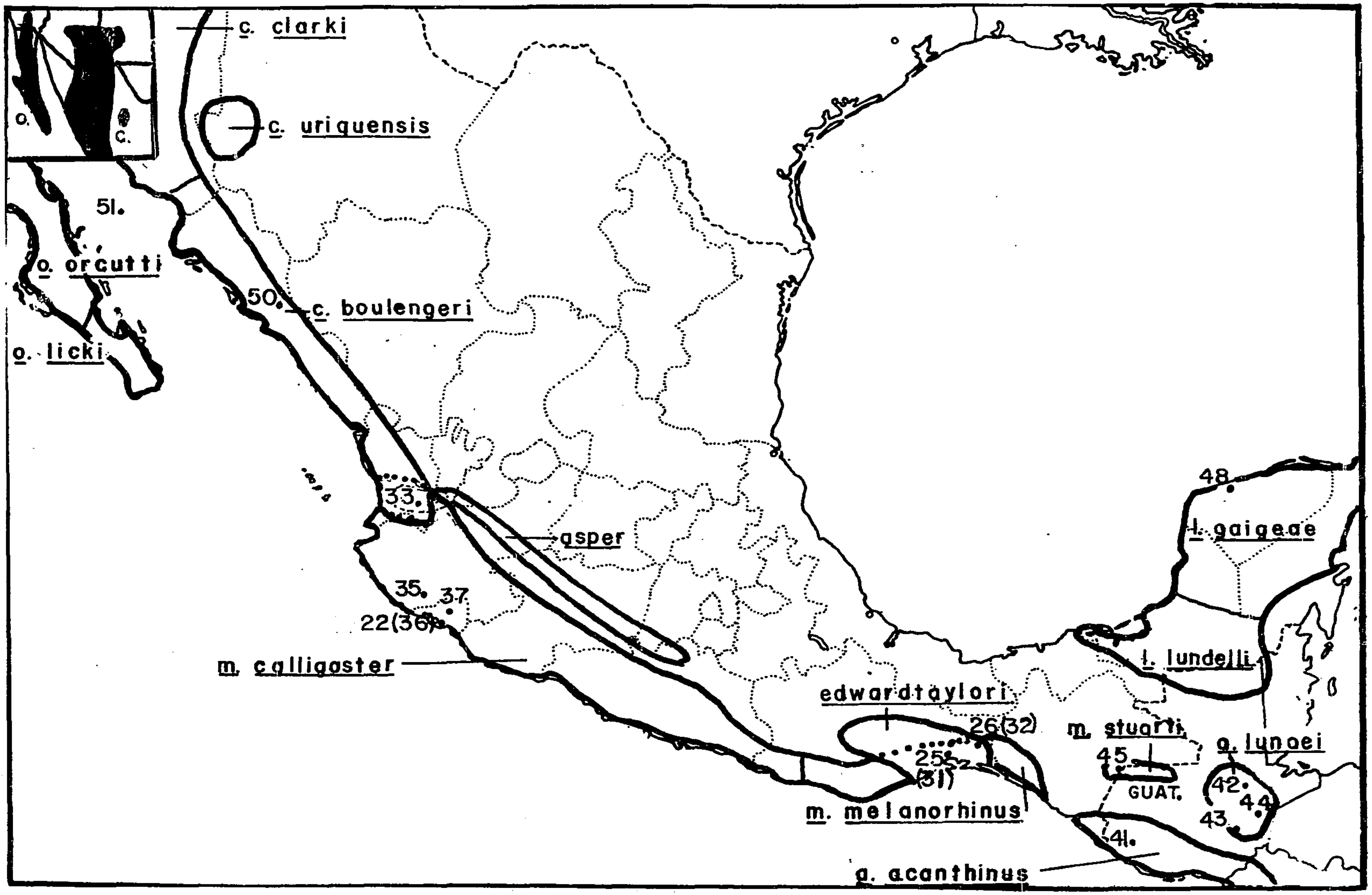

Fig. 4. Collection localities and distribution of the species of the spinosus group with uniform colored backs (orcutti, clarki, melanorhinus, lundelli and edwardtaylori) and the formosus group (asper and acanthinus) of Sceloporus.

August, 1968; February, 1969; and June, 1969. During these months, the lizards were observed almost daily during their most active periods (normally 0830-1130 and 1730-1930 CDST). In February, 1969, the activity periods were artifically induced by the heat lamps. Observation periods were never less than a half hour and usually lasted 1-3 hours. These observation periods encompassed the entire daylight period. Approximately 300 hours were spent watching their behavior. Observations were either taped and transcribed later, or taken directly as notes. Particular note was made of habitat usage and intraspecific and interspecific interactions (dominance and/or sexual) and the parameters of each. For these reasons, the lizards were held and observed in various species and numerical combinations (Table 2). In addition to these observations, another 300 hours were spent photographing the lizards' display behavior. Additional behavioral observations were incorporated into the film log to form part of the permanent record.

One characteristic of the species composing the <u>spinosus</u> group, which hindered this behavioral study, was their extreme wariness. This behavior made collecting them in the field a challenging and time-consuming task. Also, because of their wariness, observation and filming were two different activities. To observe a continuous series of "normal" activities among a laboratory population of lizards, it was necessary to use several approaches to circumvent their wariness. During filming of the lizards in the 1.3 x 1.3 m photographic terraria, all objects used to provide shelter were removed and a blind was used which shielded

Table 2. Species, subspecies and sexual composition of four enclosed lizard populations, observed in study of social behavior.

Species of	June 66		Aug. 68		Feb. 69		June 69	
Sceloporus	M	F	M	F	M	F	M	F
s. spinosus	3	3	1	0	1	0	1	0
s. caeruleopunctatus			6	6	5	6	2	5
s. apicalis			3	3	1	2	1	2
h. horridus			5	9	4	8	3	5
h. oligoporus			7	6	2	4	2	3
h. albiventris			7	4	2	2	1	2
melanorhinus calligaster			13	3	1	0		
m. stuarti							1	0
edwardtaylori			0	4	0	1		
lundelli gaigea							0	1
c. clarki	5	2						
c. boulengeri	2	2					1	0
magister uniformis	5	0					3	1
o. orcutti	0	1						
o. tortugensis	5	0						
olivaceus	18	16						
cautus	2	0						
a. acanthinus							2	2
a. lunaei							3	5
asper			1	2				
Totals:	40	24	43	37	16	23	20	26
Total hours of observation	62		42		26		89	
Days of observation	25		19		15		35	

M = Male; F = Female

major body movements. Quartz colortran flood lamps used for illumination served to prevent the lizards' seeing me in the blind's shadow. A large environmental chamber, 4 x 5.3m, provided with a port with a one-way mirror, was also used as a photographic chamber.

Indoors, an elevated platform was used for observation. The lizards were apparently not bothered by a partially shielded observer, 2 meters above them. A blind was constructed for observing lizards in outdoor enclosures. It consisted of canvas stretched over a wooden frame with a one-way mirror built into the side. Outdoors, two methods of photography were used: one was to pre-focus the camera on a site currently being used for display and then to activate the camera by cable release when the lizards were in the proper spot. This did not allow for changing light readings or for photographing other lizard activity. Also, when the spring driven camera ran down, one had to get out of the blind to rewind the camera, thus frightening the lizards. The other method was to photograph through the blind after removing the one-way mirror. By being very cautious, one could follow and photograph some lizards; but many were not deceived. A final photographic technique was to use 40 to 200 liter aquaria. This worked well on small and hatchling lizards and allowed photography at eye-level.

A Bolex H-16 camera with either a 105 mm telephoto lens or a 17-85 mm Pan Cinor zoom lens was used. The lizards were filmed with the camera running at 16 fps (frames per second) as determined by filming a stop watch and by counting the number of frames exposed during a 10-second interval. Kodachrome II Type A indoor film was used primarily.

The displays were analyzed according to Carpenter's (1962) eight categories. The data for the display-action-pattern graphs were obtained by analyzing the filmed displays frame by frame on a Bell and Howell Analyst projector, using a modification of Clarke's (1965) method. The film was projected onto a mirror which reflected the lizard's image onto translucent fadeout graph paper held by a plexiglass stand. This allowed the lizard's movement pattern to be plotted directly onto the graph paper. The plexiglass stand was positioned near the projector so the film could be advanced with one hand and the display graphed with the other. The size of the image and the amplitude of the display, as well as the position of the display, were adjusted by moving the mirror towards or away from the projector and varying the horizontal angle of incidence, the vertical angle of projection, or the height of the stand.

When the vertical movements of the display were contained within the boundaries of the graph paper, a point was selected on the lizard's head or shoulder; this point was plotted on the paper for each frame. Time was plotted on the abscissa as each division represented one frame of film (1/16 sec.). By using graph paper of eight squares/mm, ruler measurements could be converted directly into seconds by multiplying the reading in decimeters by two. The display-action-pattern graphs can then be mathematically analyzed.

CHAPTER III

MORPHOLOGY, DISTRIBUTION, ECOLOGY AND COLLECTION DATA

A brief sketch of each species in regard to pertinent morphological features, distribution, ecology and collection data are given. Of the forms studied, complete technical descriptions and habitat data are given by Smith (1939, 1946) except for the recent forms, *spinosus apicalis* (Smith and Smith, 1951), *melanorhinus stuarti* (Smith, 1948) and *magister uniformis* (Phelan and Brattstrom, 1955). The distribution maps are modified from Smith (1939). Collection localities of the lizards are presented in Figures 3 and 4. Vegetative zones to which the collection localities are assigned are based on the classification of Leopold as taken from Pesman (1962).

Spinosus Group

Sceloporus spinosus is a ubiquitous species occupying the arid central plateau of Mexico and the plateau of the state of Oaxaca. It is a characteristic species of the mesquite-grassland zone, but it is also found in the desert zone and the arid semi-cleared low areas of the pine-oak forest zone. Specimens of all three subspecies were obtained from a variety of localities and habitats (Appendix II and Figure 3). It is primarily a terrestrial species with an activity center on a boulder, tree or fence post. Specimens of *s. spinosus* were taken from rocky hillsides where they were associated with large boulders and agave. Near the city of San Luis Potosi, they were found on cement fence posts and fled under spiny vegetation when approached. The easiest collection of these wary lizards occurred when the car was used as a moving blind and they were noosed from roadside rocks and brush near Ixmiquilpan, Hidalgo.

Sceloporus s. caeruleopunctatus was associated with roadside boulders and brush south of the city of Oaxaca. They were also found on isolated trees bordering farm lands there. These thorny trees were honeycombed with natural cavities in which the lizards hid. Previously, this subspecies had only been reported on rocky habitats (Smith, 1939). Though they were found on trees, their escape behavior was that of a terrestrial species. When pursued, they fled into the cavities rather than fleeing up the tree. This behavior seems analogous to a terrestrial species escaping beneath a boulder as both flee to a darkened hole.

Specimens of *s. apicalis* were taken from a rocky, scrub tree hillside 30-50 km south of Oaxaca, Oaxaca. Here they were associated with agave bases, boulders and low thorny trees.

Morphologically, the subspecies of *spinosus* are practically identical except for minor scutelation differences (Smith, 1939; Smith and Smith, 1951). The general pattern is prominent light dorso-lateral stripes on a dark brown background and is similar for both sexes. A series of light bars (narrow in males and wider in females) are present down the back. Prominent ventral features on the throat of both sexes are blue or black bars which converge to a median blue patch in males. Males also have two separate ventro-lateral blue belly patches which darken medially to black. Females lack the blue ventral coloration. Males also have blue spotted scales grouped as a series of irregular paired dots down the back.

Dorsally, the 3 subspecies of horridus are almost indistinguishable from each other and from spinosus. For this reason and their allopatric distribution, some have considered the species to be conspecific, but Smith (1939) considers them distinct. While horridus and spinosus form a homogeneous grouping on the basis of gross morphology and dorsal colorations, they can easily be separated on the basis of femoral pore counts and ventral coloration. All spinosus have a total of more than 13 femoral pores while all horridus have a total of less than 13. Sceloporus h. oligoporus and h. albiventris have a total of less than six femoral pores, while h. horridus has more than six. Sceloporus h. albiventris is distinct because the males lack the ventral blue coloration. This unique feature is shared within the spinosus group only with edwardtaylori.

The ventral coloration of h. oligoporus was variable. While reported to be less intense than that of h. horridus (Smith, 1939), it appeared just as vivid in active individuals. However, in the laboratory, when male h. oligoporus were cool or inactive, such as when first observed in the mornings, their ventral coloration was faded and very pale. On either warming or becoming active, the male's ventral coloration deepened to the brilliant blues characteristic of the subspecies. This variability of color pattern needs further work to determine the factors which influence the intensity changes. This phenomenon might be similar to a light stimulated raction observed in male Red River Pupfish, Cyprinodon rubrofluviatilis, their breeding coloration is light dependent, fading at night or in darkness (Echelle, pers. comm.).

Sceloporus horridus was opportunistic in its habitat preference. It was abundant in both strictly arboreal and in rocky habitats. Lizards were collected off several kinds of trees, boulder strewn pastures, candelabra cactus, rock walls and road cuts. All habitats held in common two things, an elevated site and a retreat or hiding place.

Specimens of h. horridus were taken off tall salt cedar trees (Tamarix sp.), thorn trees and rock walls near Cuernavaca, Morelos. Sceloporus h. albiventris near Tepic, Nayarit, was found abundantly on isolated boulders in roadside brush pastureland which was either cleared arid scrub or pine oak forest at about 1,000 m. Some were also seen in Tepic on salt cedar trees and rock walls. However, it was rarely observed in the woods; only 3 individuals were seen deep in the pine oak forest, and in both cases they were associated with rock walls.

Over much of its range, the distribution of horridus overlaps melanorhinus (Figures 3 and 4), but they were collected together in only four of ten possible joint collection sites. In only one, site 37 near Colima, Colima, were both abundant. Because of their distributional pattern and their habitat similarities, it appeared that horridus was in competition with melanorhinus. Above 500 m, the former was abundant while below 500 m, the latter was more common. Away from the coast, h. oligoporus was found abundantly on the same species of tree, Astranthus viminules, that melanorhinus inhabited exclusively on the coast. Near the city of Colima, in roadside thorn trees, both species were found; horridus was slightly more abundant (7/4). They were not observed together on the same tree and h. oligoporus appeared more terrestrial than melanorhinus as it was observed several times on the ground and took refuge in burrows. However, horridus often behaved as melanorhinus did by fleeing up the tree out of reach.

At Zihuatenajo, Guerrero, two h. oligoporus were caught off large trees bordering a coastal stream bed. One melanorhinus was also taken there, but neither species was abundant. In the Tepic, Nayarit, area, two melanorhinus were taken from oak trees bordering a stream at about 1300 m. At nearly the same elevation, but on cleared pastureland, h. albiventris was abundant on boulders while only three of over 100 of these lizards were observed on trees. However, in addition to possible competition by melanorhinus, six other arboreal species were seen in the area, two of which, clarki and asper, are closely related.

Sceloporus olivaceus, the Texas spiny lizard, was collected in the Dallas-Ft. Worth, Texas, area from various city parks and open woodlands. This species was strictly arboreal. Since the display of this species had been previously analyzed (Bussjaeger, 1967), these specimens were obtained for observing their social behavior.

Additional descriptions of olivaceus are given by Blair (1960), who did a complete life history study of a population of these lizards. Sceloporus olivaceus belongs to the dorso-lateral striped group. Their general coloration is brownish. They have a sexually dimorphic dorsal pattern; females have eight transverse bars across the back, while males have prominent dorso-lateral light stripes as their bars have faded. In addition, only males have a rusty brown nape and separate, rather restricted, ventro-lateral blue patches.

Three other species found in the United States compose the spinosus group: magister, clarki and orcutti. The first belongs to the group with dorso-lateral stripes while the latter two belong to the series with uniform colored backs. Since their social behavior and display patterns were analyzed by Bussjaeger (1967), these were used to study interspecific behavior. Recent descriptions of these species are given by Stebbins (1966). The female coloration is similar in all species, but the males are distinct. Basically, magister is brownish, darker on the sides than above, with a prominent black wedge-shaped mark on each side of the neck. Sceloporus clarki is gray or bluish green above with black bands on the wrists and forearms. The gound color of male orcutti is copper, but they are most distinct because they are dark-colored dorsally with a broad purple stripe. Males of these three species have extensive brilliant blue throat and belly patches, but their ventral coloration is specifically distinct.

Smith (1939) considered cautus to belong to the undulatus group, of which it would be a relatively large lizard (up to 80 mm s-v length). Sceloporus cautus is characterized by a light olive-gray color with two weak dorso-lateral light stripes and a series of dark spots on either side of the dorsal line. Females have 9-10 bars across the back and no indication of a dorso-lateral light line. Ventral coloration of the males consists of two lateral blue belly patches. Smith (1939) considered the undulatus group to be derived from the spinosus group (Fig. 1) and cautus to be the form connecting the two groups. Recently, Hall (pers. comm.) stated cautus to be the same species as olivaceus on the basis of karyotypes and the discovery of an intermediate population in the valley between Saltillo and Monterrey in northern Mexico. Smith (1939) did not consider the possible relationship of these two forms; he did indicate that both are distinct from spinosus. The following characters of cautus and olivaceus appear to indicate that they are geographic variations of the same species as the characters are either the same or grade into each other (Table 3).

Only two small males were available for study. They were taken about 130 km apart in northern San Luis Potosi and southern Nuevo Leon in the mesquite grassland zone. Since they were found on the ground near brush, their habitat preference seems similar to other members of the undulatus group which are primarily ground dwellers.

Sceloporus melanorhinus belongs to the uniform back line

Table 3. Comparison of characters possessed by S. cautus and S. olivaceus.

	Character	cautus	olivaceus
1.	Widely separated blue belly patches.	yes	yes
2.	Dorso-lateral stripes predominant in males.	yes	yes
3.	Female distinctly barred, lacking dorso-lateral stripes.	yes	yes
4.	Dorsal cross bands.	9-10	7-8
5.	Black lines on posterior of thigh.	yes	yes
6.	Supra-ocular scales.	5-6	5-7
7.	Femoral pores.	10-14	11-16
8.	Dorsal scale count.	31-39	28-33
9.	Strongly mucronate scales.	yes	partially
10.	Median auricular lobules large.	yes	yes
11.	Habitat preference.	ground	trees
12.	Similar display-action-patterns.	yes	yes

(lacking prominent dorso-lateral stripes). The male has a gray dorsum; the female is brownish with a dorsal series of indistinct black bars. Compared to others of the spinosus group, they have several unique features of coloration. Both sexes exhibit a head pattern which consists of two black bars, one on the nares (hence their specific epithet), and another on the head shield. These bars are separated by a white line, bordered by black below, which extends backward past the shoulders. The male's ventral coloration is unique. His ventral surface is orange with a single blue throat patch and separate ventro-lateral blue belly patches. The throat patch is bordered by black posteriorly. The sides of the abdomen have a yellowish cast. Females lack the ventral coloration, but have yellowish sides.

Sceloporus melanorhinus was found at seven localities within its range (Fig. 4). It was found abundantly only at two coastal sites near Manzanillo, Colima. A moderate number were seen near the city of Colima, but at four other sites, no more than two individuals were observed.

Apparently the habitat of this species is strictly arboreal and limited further to low elevations (usually less than 1000 m). The two large populations were associated with the yellow-grass tree, *Astranthus viminules*, in a dry coastal stream bed. This tree, physiognomically similar to a large willow (*Salix* sp.), had rough gray bark which perfectly matched this lizard's coloration and offered an excellent climbing substrate. *Sceloporus melanorhinus* was also collected inland on oaks (Tepic, Nayarit, 1200 m), and on thorn trees (Colima, Colima and Uruapan, Michoacan, 500 m). Inland, as discussed previously, *melanorhinus* was apparently displaced by *horridus*.

Sceloporus edwardtaylori is a large species--up to 112 mm in snout-vent length. A member of the uniform back group, it is a gray lizard characterized by immaculate ventral surfaces in both sexes. The broad gray dorsum of *edwardtaylori* is bordered by two indistinct lateral stripes of darker slate. Irregular dark markings separated by a lighter band are present dorsally.

All specimens used in this study were collected at two sites separated by 60 km--one site 11 km south of Tehuantepec, Oaxaca; the other 50 km east of this city (Fig. 4). This lizard is exclusively arboreal. Because of the aridity and land use, most trees were small and scrubby; most of the lizards were seen on large rough gray-barked trees bordering fields and pastures of this tropical deciduous forest zone. Adults were usually first observed 3-5 m up the main trunk and sometimes as high as 10 m. Normally, the lizards were found basking on trees at the edge of groves. Ground cover beneath the trees was usually barren or sparse shrubs or grass. Because of cultivation, most of the habitat was either savannah-like or small cleared farmlands in a scrub forest.

Sceloporus lundelli was represented by one female of the subspecies *l. gaigeae*, collected by Jeremy Penner near Progreso, Yucatan (Fig. 4). It is reported to be a secretive arboreal species. This *spinosus* group member belongs to the series with uniform backs. Males have a uniform olive-gray dorsum with a black spot anterior to their forelegs. They have black bordered ventro-lateral blue belly patches which fuse medially on the chest and belly. The males also have a median blue throat spot situated on a light orange field. Females are grayish with four narrow undulate dark gray bands across the back and lack the ventral coloration of the male.

Formosus Group

Sceloporus asper was one of the three members of the *formosus* group obtained in this study. Three individuals of this arboreal, mountain-dwelling species were taken from an open oak woodland, 35 km east of Tepic, Nayarit, Mexico (Fig. 4). Only four were found even though three days were spent searching for this species. This agrees with Smith (1939); he said they were illusive, scarce, and secretive and they were normally seen fleeing high up a tree.

As typical of the formosus group, the general dorsal coloration of the male asper was greenish. Females of asper were first mistaken for oddly colored female melanorhinus; they were recognized as distinct only when the male was taken. In addition to the greenish coloration, the male is characterized by lacking blue throat patches and having two separate ventro-lateral pearl blue or pale blue belly patches. Sceloporus asper is a small lizard, as its maximum snout-vent length is 81 mm (Smith, 1939). Available specimens were slightly smaller. However, acanthinus of this group attains the same size as those species in the spinosus group.

Sceloporus acanthinus lunaei was restricted to the eastern mountain slopes of Guatemala, primarily east and southeast of Guatemala City (Fig. 4). Specimens of this species were obtained from three localities: Salamá, Jalapa and near Jutiapa, Guatemala. The habitat at the Salamá site consisted of log piles and roadside trees. At Jutiapa and Jalapa, the habitat was fence posts, small boulders and rocky roadcuts. This subspecies seems more terrestrial than a. acanthinus. Collection localities as well as distribution maps are given in Figure 4 and Appendix II.

The male's dorsal coloration is greenish--each dorsal scale having a bright chartreuse spot on it. Ventrally, males have separate black bordered blue-green belly patches and a single medial throat patch bounded posteriorly by black which extends onto the shoulder as a blotch. The females are unpatterned dark gray-brown with two series of ten dark spots down the back. Neither sex suggests the presence of a dorso-lateral line so characteristic of the *spinosus* group.

Sceloporus a. acanthinus is restricted to the Pacific slope of Guatemala (Fig. 4). Individuals used in this study were collected 30 km west of the junction of hiways 6W and 9S. Their habitat was a tall grove of willow-like trees with lancelate leaves and rough dark gray bark. The coloration of *a. acanthinus* was similar to that of *a. lunaei*, the primary difference was that both sexes of *a. acanthinus* possessed a broad, dark dorsal collar. They were also more greenish than *a. lunaei*, the male was bright green while the female was a dull green.

CHAPTER IV

DISPLAY BEHAVIOR OF THE SPINOSUS GROUP OF SCELOPORUS

Lizards in the iguanid and agamid families perform a rhythmic stereotyped series of movements of push-ups and head nods associated with various postural changes. These movements and postures make up the ritualized display behavior of the species. These behaviors are assumed to function in announcing the displayer to members of its species, in declaring a territory and in acting as an isolating mechanism.

The displays are analyzed according to eight categories established by Carpenter (1962a): site, position, posture, movement type, parts moved, units of movement, sequence and cadence. A verbal and graphical description of the full or challenge display is presented for each species. Variations in the displays are also presented. The total number of displays analyzed and number of individuals photographed for each form are presented in Table 1.

The postural and movement components of the display varied with the intensity level of the displayer. Since there was a continuous range of intensity levels, the range has been divided to indicate the two major functional attributes of the display. The high intensity display (challenge) was restricted to the full complete display and contained extreme movements and all postural components--dewlap extension, lateral compression, arching of the back and lowering of the head--and usually orientation of the display towards a similar sexed member of the species. The challenge display was given usually in conflict situations during dominance determining or maintenance situations. As a working definition, any display with extreme posturing was called a challenge display. Ideally, it would apply only when the display was oriented to another lizard, but because of the difficulty in determining if the display was oriented, all full postured displays were considered challenge displays. The low intensity (assertion) display usually lacked postural changes and was the display performed in non-conflict situations and even by isolated lizards. All non-challenge displays were termed assertion displays. Thus, an assertion display included a variety of intensity levels. The following scheme, which lists the major intensity levels seen in the displays of the <u>spinosus</u> group, illustrates this definitional separation. From lowest to highest intensity, as evidenced by subjective evaluations of their postural changes and the degree of vertical movement, the categories are:

A. Slight movement of head and body.

B. Partial extension (½) of forelegs--no postural changes.

C. Full extension of forelegs.
    1. No postural changes (normal assertion display).
    2. Postural changes.
        a. dewlap out
        b. sides compressed
        c. both of above, but not full extension

D. Full or extreme leg extension and posturing, with or without orientation (challenge display).

Because of the context in which members of the spinosus group performed displays, a slightly different scheme of identifying the intensity levels is used than proposed by Carpenter (1962a) for undulatus. He called intensity level D, the challenge display and levels C1 and below, the assertion display. The C2 levels, although probably not extensively observed or performed by the smaller undulatus, would probably be placed in the challenge display category. In this study, the D intensity level was also termed the challenge display, while the C2c level and below were termed assertion displays. Almost always, the C2 displays were performed by high ranking lizards in the enclosure.

One could subdivide the above categories further by considering degrees of dewlap extension or lateral compression. The display of a lizard usually changes from one display type to another, usually from a higher to lower intensity form. Therefore, the initial attitude was most useful in classifying the display. These artificial intensity categories could be used to correlate postural changes and body movements with the form of the display-action-pattern graph, number of units, or dominance status.

As indicated by the categories, a verbal description of the display would vary with intensity. However, the graphical description of the display was practically the same at all intensity levels and no major differences have been noted between the form, shape or cadence of the display-action-pattern graph. However, in the challenge display, the vertical movements were of greater amplitude and the display sequence included more repeated units. For these reasons, the displays were described on the basis of the challenge displays while all displays were used in determining the display-action-pattern.

In *Anolis* sp., display-action-patterns were different for their assertion and challenge displays. Their challenge displays were variable while the assertion displays were simpler and more consistent. Littlejohn (1969) commented that as a characteristic to be used as an isolating mechanism or as a species-specific communication signal, the assertion display should ideally be used between members of a species. The assertion display was performed more often and would be the one performed by males to females. On these bases, Jenssen (1969) studied the assertion display of *Anolis nebulosus* in making his quantitative study of the variation in its display. This extreme variation in the challenge display and between the challenge and assertion display was not true of the *spinosus* group of *Sceloporus* (or any other known iguanids). This difference between *Anolis* and *Sceloporus* may be related to the retention of the signal function of the display in the push-up by *Sceloporus* while in *Anolis* the dewlap might have assumed this function. Thus, the variable display patterns of *Anolis* might be the result of a lack of selective pressure for signal specificity. One similarity in the *spinosus* group was whenever an individual performed an aberrant display it was invariably a challenge display.

Display of Spinosus Group of Sceloporus

The displays of the spinosus group of Sceloporus were typical of the Iguanidae. Except for the display-action-patterns, the displays were not significantly different from those previously described for Sceloporus undulatus (Carpenter, 1962a) or for the other spinosus group species (Bussjaeger, 1967). Minor differences of each form from the following generalized description will be given in the species account, where Carpenter's last three categories of display analysis, those associated with the display-action-patterns, are discussed.

Site.

All forms showed a marked preference to display from elevated sites in their natural habitat which afforded them a wide field of view. Depending upon their habitat preference, this would be a top of a boulder, rock wall, fence post or exposed part of a tree trunk, or a branch. It would also be an expression of their normal preference for a basking, resting or lookout perch. In the laboratory, raised sites provided in the enclosure were utilized as in the field for display sites. Depending upon the normal habitat preference (rock vs. tree) of the species, a similar preference was exhibited in the enclosure. The arboreal forms (melanorhinus, asper, edwardtaylori, a. acanthinus, a. lunaei and horridus oligoporus), preferred the tree limbs and posts in the enclosure for display sites while the terrestrial forms (magister, spinosus and h. horridus and h. albiventris) preferred the rock piles. Neither preference was absolute, but the arboreal species showed a greater preference for the tree-simulating objects.

Although most displays were performed on elevated sites, the lizards displayed on the floor of the enclosure--primarily while enroute from one raised site to another, while at the food pile or while chasing another lizard.

Position.

The body of a challenge-displaying lizard was held almost parallel to the substrate with the anterior higher than the rear, at an angle of 20-30°. Most displays were performed in the horizontal positions on the top of rocks or branches, but all species did push-ups on the vertical face of rocks or trees, either with the head up, head down or with the body at various angles and even upside down. The arboreal forms performed most of their displays in a vertical position.

In a challenge display, the primary orientation was towards the recipient of the display. The lizards oriented their bodies laterally toward the adversary and tilted their body axis to present the side of their body perpendicular to their opponent's view. When fighting, the lizards assumed face-off positions towards one another, presenting their bodies laterally--either with their heads facing the same or opposite directions. During the latter as the opponents circled, the orientation of the display might become almost cephalad as the body axis of one turned perpendicular to the body axis of the other.

Posture.

In a challenge display, the lizard exaggerated its body posture by compressing its sides, arching its back, extending the dewlap and lowering the head. This posturing made the lizard appear larger and present its ventral coloration to the opponent. Concomitantly, the lizard raised its body on extended fore and hind legs. The ventral coloration is thought to be a sign stimulus that functions to intimidate subordinate males and/or to aid in male recognition (Carpenter, 1962a). The ventral areas were only presented by the dominant lizard--whom, in effect, had declared the enclosure as his territory--or by males recently introduced whose status ~~in the dominance hierarchy was being~~ established.

In the *spinosus* group of *Sceloporus*, the head was usually held in the normal axis which was a straight extension of the midline of the body. It might be slightly bent toward the challenging lizard, but normally it was parallel to the other lizard's body. The mouth was normally closed. The dewlap was extended and there were slight differences in the shape and color of the dewlap between species. The tail was normally laid flat, trailing behind the lizard. Depending on the species, the lizard began the display in either the raised or lowered position.

Movement type and parts moved.

The movement was a push-up accomplished with the extension and flexion of the fore legs. The head and fore part of the body acted as a rod pivoted on a fulcrum provided by the partially extended hind legs. The push-up display consisted of a series of up and down movements that formed a unique temporal pattern for each species.

Units of movement.

The display was subjectively divided into units for analysis. Following the definition of Clarke (1965), a unit was composed of two parts, the push-up and the pause. The push-up consisted of a major upward movement and a major downward movement to near the original low position; then there was a pause or freeze until initiation of the push-up of the following unit. The push-up movement might be in the form of a single peak, double peak or something more variable depending upon the movement path traced by the displaying lizard between the major vertical movements. A single unit was one whose push-up movement was an up, hold, and down and then a pause. A double unit consisted of an up, slight lowering and rise and then a down and pause at the original level. In general, most units performed by the *spinosus* group of *Sceloporus* were single units, but the form of the single unit was quite variable.

Sequence of Movements.

The arrangement of the different types of units described for each species was nearly constant. Most variations were primarily in the number of units which depended upon the individual's social status, intensity of the display and the species. To analyze the displays, each unit was numbered consecutively from the initial push-up movement. Within each unit, the push-up movement was termed "a"; the pause termed "b". Some individuals performed displays with additional units inserted between the normal units, these were given prime number designations, e.g. 3' for a unit between units 3 and 4. Also, when some individuals introduced their display with additional units, they were labeled alphabetically from unit 1, from right to left, e.g. C, B, A, 1, 2, 3 etc.

Also, for comparing the total number of units performed in a display, the term, median terminal unit (abbreviated MTU), was used. It means the last unit of the display of an individual or group average in which at least one-half of the total displays have terminated. Since both assertion and challenge displays were analyzed together it was a more accurate estimate of an "average" display than using the mean of the total number of units performed. Ideally, with a large sample of each of the previously stated intensity categories, one should be able to calculate a significant mean number of units performed for each level. The present sample size necessitated lumping these data.

A display may be "complete" and contain all the different units of the display or it may contain only a portion of the display, thus being "incomplete". If the units of an incomplete display could be recognized, they were analyzed. All terminal units or parts of the unit were included in the analysis, unless the termination unit was aberrant. Thus, if the unit was different than when this same unit was included in the body of the display, it was not analyzed. In describing the sequence of movements, Carpenter (pers. comm.) classifies displays into two broad categories: determinate and indeterminate. Determinate displays consist of only a set combination of units which are repeated. An indeterminate display consists of an introductory series of nonuniform units followed by a series of either a repeated unit or units, the number of sets of these repeated units being quite variable.

Cadence

Total times for each unit and for the total (MTU) display were determined from films. The timings were characteristic for each species. Unless stated otherwise, all displays presented for individuals are averaged displays. Because of the unequal number of displays obtained from each individual, and since each individual's display was usually distinct with little variability, the generalized species and subspecies displays were determined by averaging the individual means.

Species Display

Sceloporus spinosus

Although unequally represented, all three subspecies of *spinosus* were sampled. Their displays were very similar. The displays consisted of a series of single units which varied primarily in length from initial longer units to shorter terminal ones. Displays of *s. apicalis* and *s. caeruleopunctatus* appeared identical while those of *s. spinosus* were different. The displays of *s. spinosus* differed in that its units always contained a pause (part "b") while the other subspecies lacked this pause in the last units of their display.

Forty-seven displays were obtained from eight *s. spinosus* collected from three localities (Fig. 3). Forty-two displays followed the general pattern (Fig. 5A). The generalized pattern consisted of a short single push-up and pause for the first unit, then two long single units with very short pauses between the push-up movements and then a series of almost identical units. These latter units shortened as the display proceeded. Very little variation was evident between displays of an individual or between individuals, except for a few instances detailed below. The generalized (MTU) display contained five units and lasted 7.78 seconds; a nine unit display lasted 11.40 seconds.

Three individuals performed five alternate "aberrant" displays (Fig. 5B). The most unusual aspect of these displays was that the same variation occurred in three individuals collected from two localities. Apparently this pattern variation was also characteristic of this subspecies. This display pattern began with three almost normal units. However, the fourth unit push-up movement was sharp-peaked with a relatively long pause. The fifth unit was a double-peaked unit with a low plateau and short pause. The sixth unit appeared normal, with a long pause, but the seventh unit was a single-peak. This unit might have been a partial unit as it was based on only one display. All five displays included the fifth unit, and the sixth unit was observed twice.

Normally little variation in a species display was found. Most variations were apparently isolated aberrant displays. The two _S. spinosus_ which showed the greatest amount of variation in their displays were female _br_ and male _byb_. Each performed three

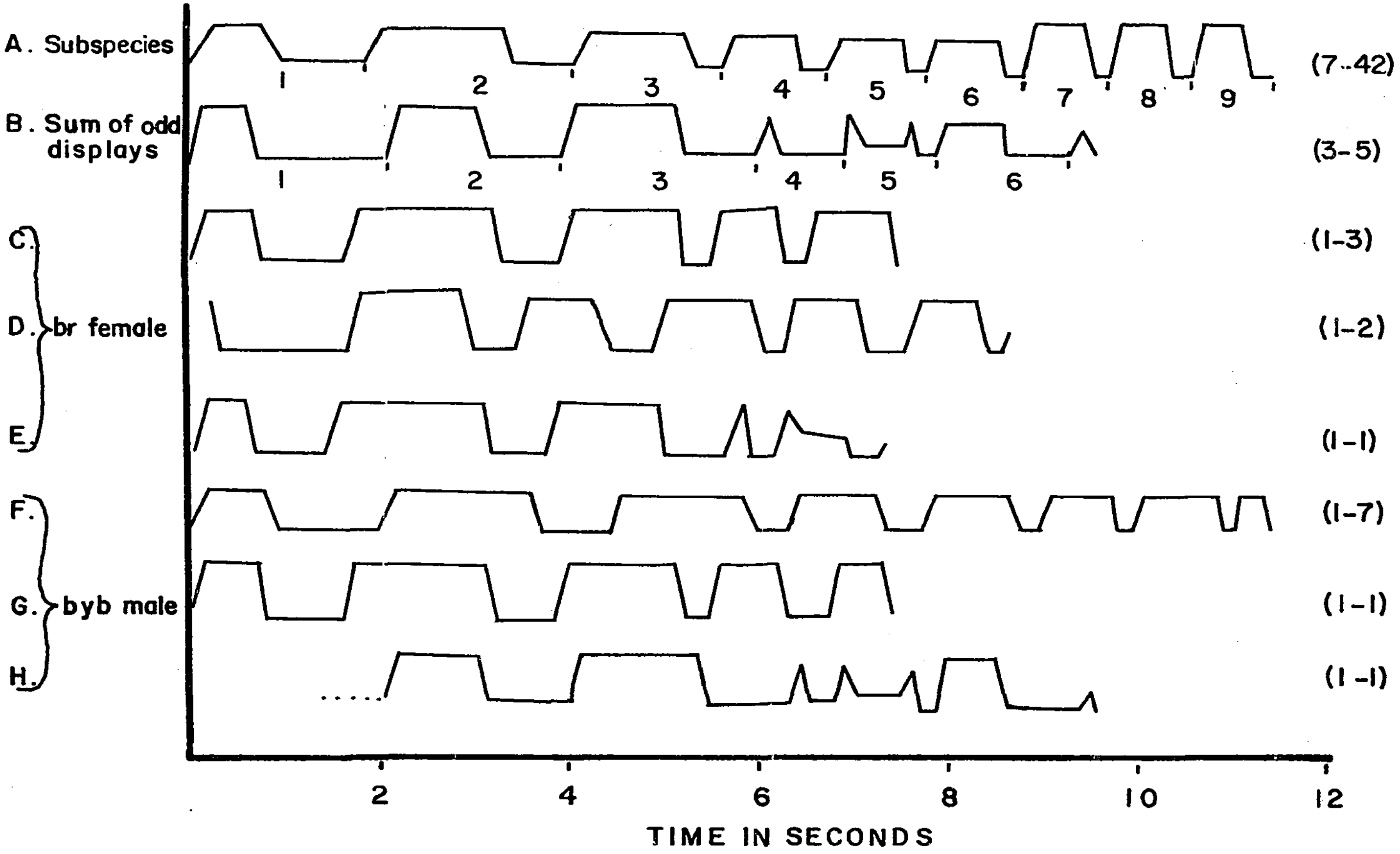

Fig. 5. Display-action-pattern graphs of <u>Sceloporus</u> <u>s</u>. <u>spinosus</u>. Lines represent relative up and down push-up movement through time. Units of measurement are indicated beneath the graph. Numbers in parentheses refer to the number of individuals and displays, respectively, upon which the graph is based.

different patterns (Fig. 5), but the different patterns were performed very few times. The greatest amount of variation found within one display type was illustrated by br female (Fig. 5C, D). Both were variations similar to the species display (Fig. 5A). The first, display C, was performed three times; the other, display D, was performed twice. The major difference was that units 2 and 3 were shortened in display D. Whether this was a fixed variation as hypothesized for the B display or just an inconsistency in the display could not be determined by this small sample.

Three display patterns were also performed by byb male. The aberrant (B) pattern was performed once (Fig. 5H). His averaged normal display pattern (Fig. 5F) and the most variant of his species displays (Fig. 5G), are presented. The latter was similar to br female's "C" display. The major difference between the averaged display (F) and the actual display (G) was that "G" occurs at a faster cadence. In this subspecies, units 1 and 3 appeared to be the most variable.

The displays of the subspecies s. caeruleopunctatus and s. apicalis were analyzed together. This was because of the large percent (37%) obtained from individuals which were intergrades between the two subspecies in morphological characteristics as well as distributionally and the similarity of the displays. The only suggested difference between their displays was that the southern subspecies, s. apicalis, seemed to perform its displays at a faster cadence, but a larger sample is required to test this difference.

Eleven individuals of these two subspecies performed 100 displays. These individuals were collected south of Oaxaca in an 80 km transect to the type locality of s. apicalis. Five s. caeruleopunctatus performed 56 displays; two s. apicalis performed one display each; four intergrades performed 37 displays, and five displays were performed by unknown spinosus subsp. (Fig. 6).

The general form of these displays was similar to s. spinosus except most lizards omitted the pauses between the push-up movements of the latter units (Fig. 6). The presence or absence of pauses was variable. All lizards performed some displays with pauses in some of the units; others always had pauses and others omitted pauses in all units.

The display pattern consisted of single units--an initial medium length unit, a long unit, then a series of progressively shorter units. About one-fourth of the time, as the display progressed, the base line would elevate so the relative vertical movement was less (Fig. 6H). Individuals performed displays both with a constant base line and an elevating one.

The averaged displays of several individuals and the generalized display for the subspecies were all similar (Fig. 6). The greatest variation found within one individual's display was that of wb male (Fig. 6K, L). The longest display contained 16 units and lasted 13.3 seconds. The MTU as well as the terminal modal unit for the 100 displays was unit 6 and lasted 9.84 seconds.

Sceloporus horridus

A total of 284 displays performed by 34 individuals

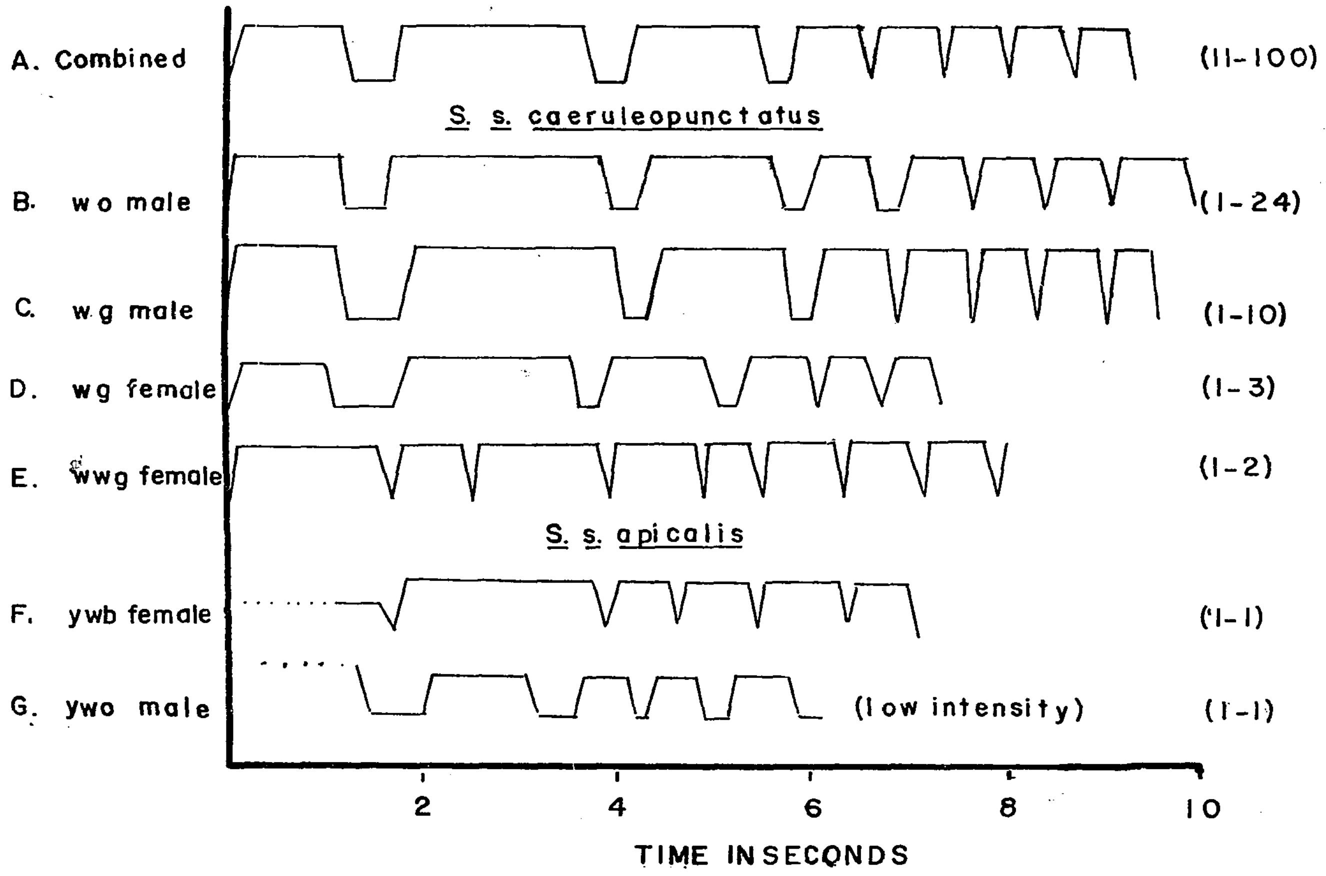

Fig. 6. Display-action-pattern graphs of S. spinosus caeruleopunctatus and S. s. apicalis. Combined subspecies display is presented with the displays of pure s. caeruleopunctatus (B-E), pure s. apicalis (F-G) and intergrades (H-L). See Figure 5 and text for explanation.

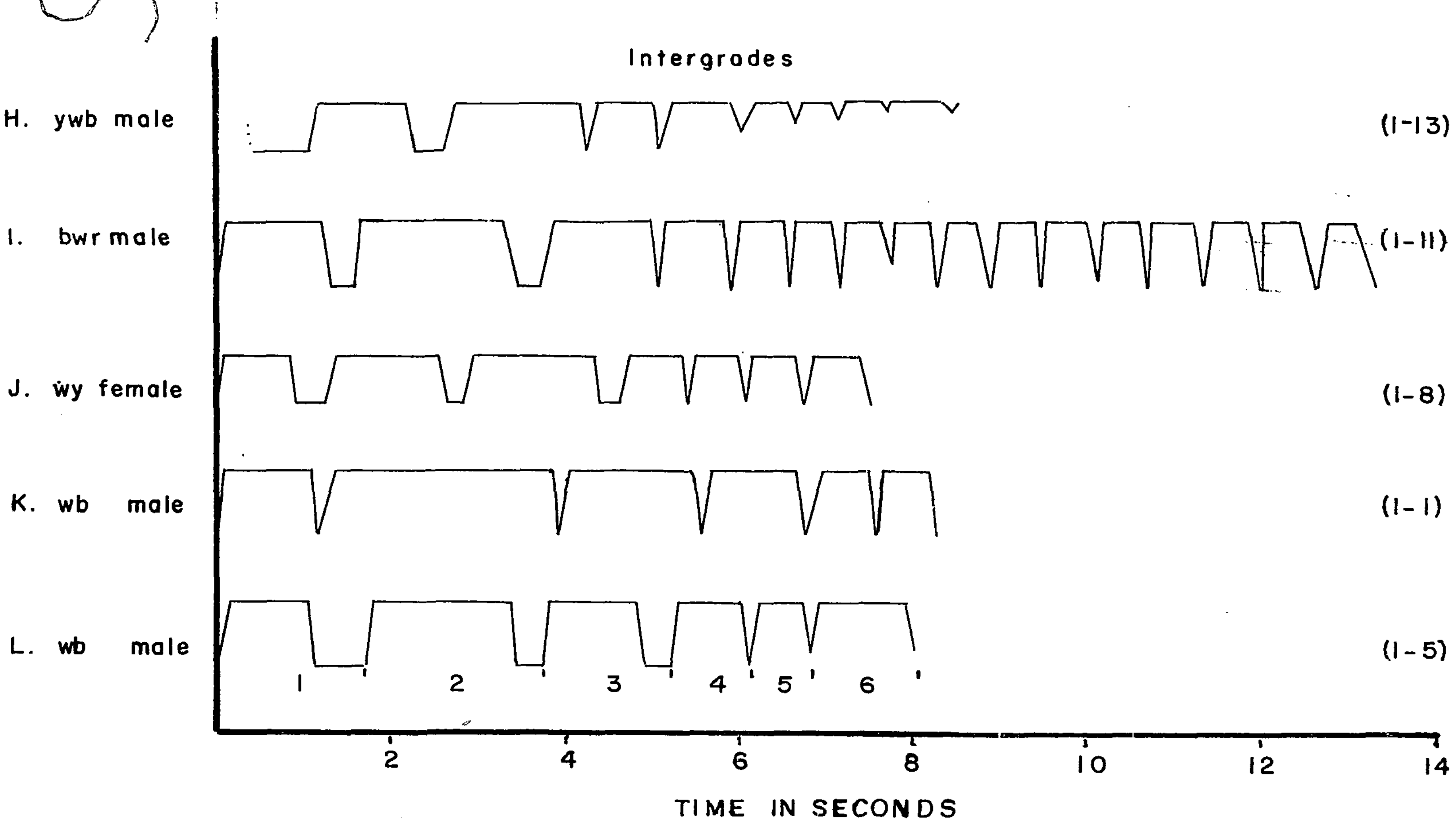

Fig. 6. Continued.

belonging to three subspecies was analyzed in studying the display of *horridus*. The displays were consistent with the general description given for the first five categories of display analysis.

The display consisted of a series of single units (Figs. 7, 8, 9, 10). However, the displays of *horridus* were unique in that three slightly altered display patterns were fixed in the species (two in each subspecies). Subspecific and populational differences were suggested in the display of *horridus*. The two display forms found in *h. oligoporus* and *h. albiventris* were almost identical and were arbitrarily called *A* and *B*. The two display forms of *h. horridus* were designated *A'* and *C'* as they varied from the other subspecies. Form *A'* was very similar to their *A* form, but the *C'* form was distinct from their *B* form. The *A* pattern (Figs. 8, 9, 10) consisted of alternating shorter and longer units. The *A'* display of *h. horridus* was slightly different in that its unit 3 was longer than the following unit, thus interrupting the repeated pattern of shorter and longer units (Fig. 7A). Otherwise, it was identical to the *A* pattern and thus it was not considered a major pattern variation. The second major pattern, *B*, was also characteristic of *h. oligoporus* and *h. albiventris*. It appeared as a series of nearly identical equal length single units after an introductory series of three single units with exaggerated pauses (Figs. 8B, 9B). Also, after the introductory series, the single units were slightly clumped as pairs--4 and 5, 6 and 7. The third pattern, *C'*, was unique for *h. horridus*. It consisted of three comparatively long introductory single units

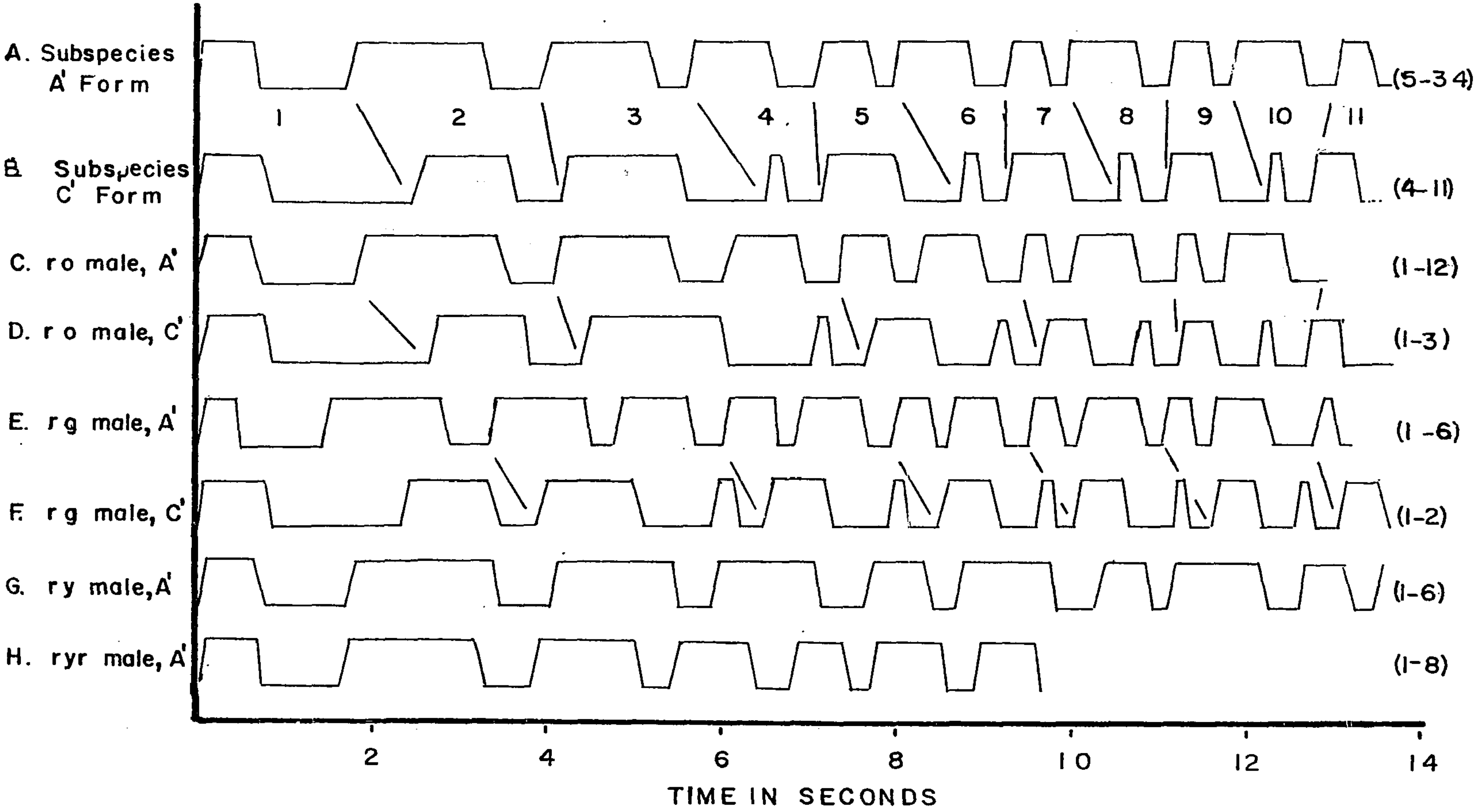

Fig. 7. Display-action-pattern graphs of Sceloporus h. horridus. See Figure 5 and text for explanation.

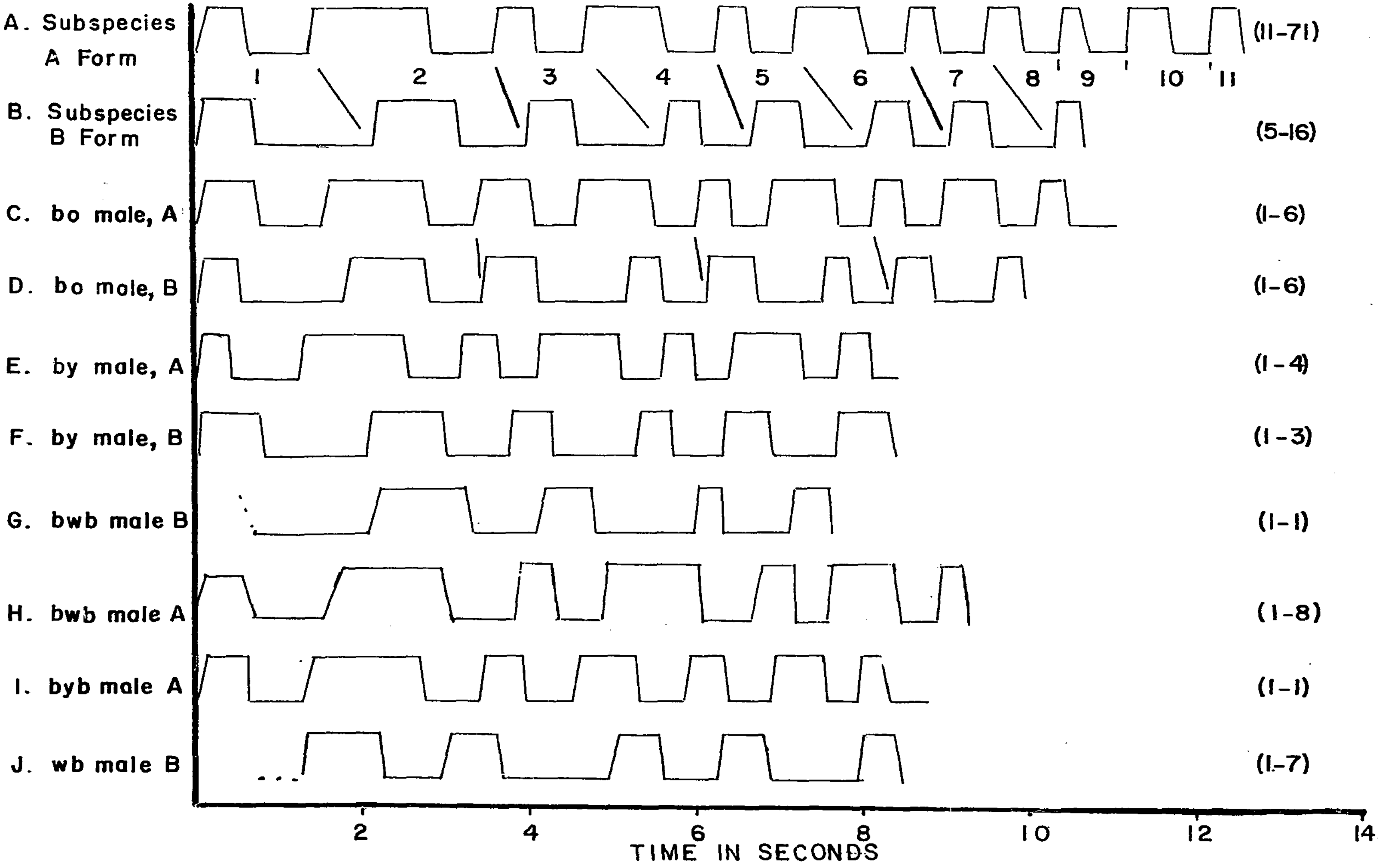

Fig. 8. Display-action-pattern graphs of *Sceloporus* *h*. *albiventris*. See Figure 5 and text for explanation.

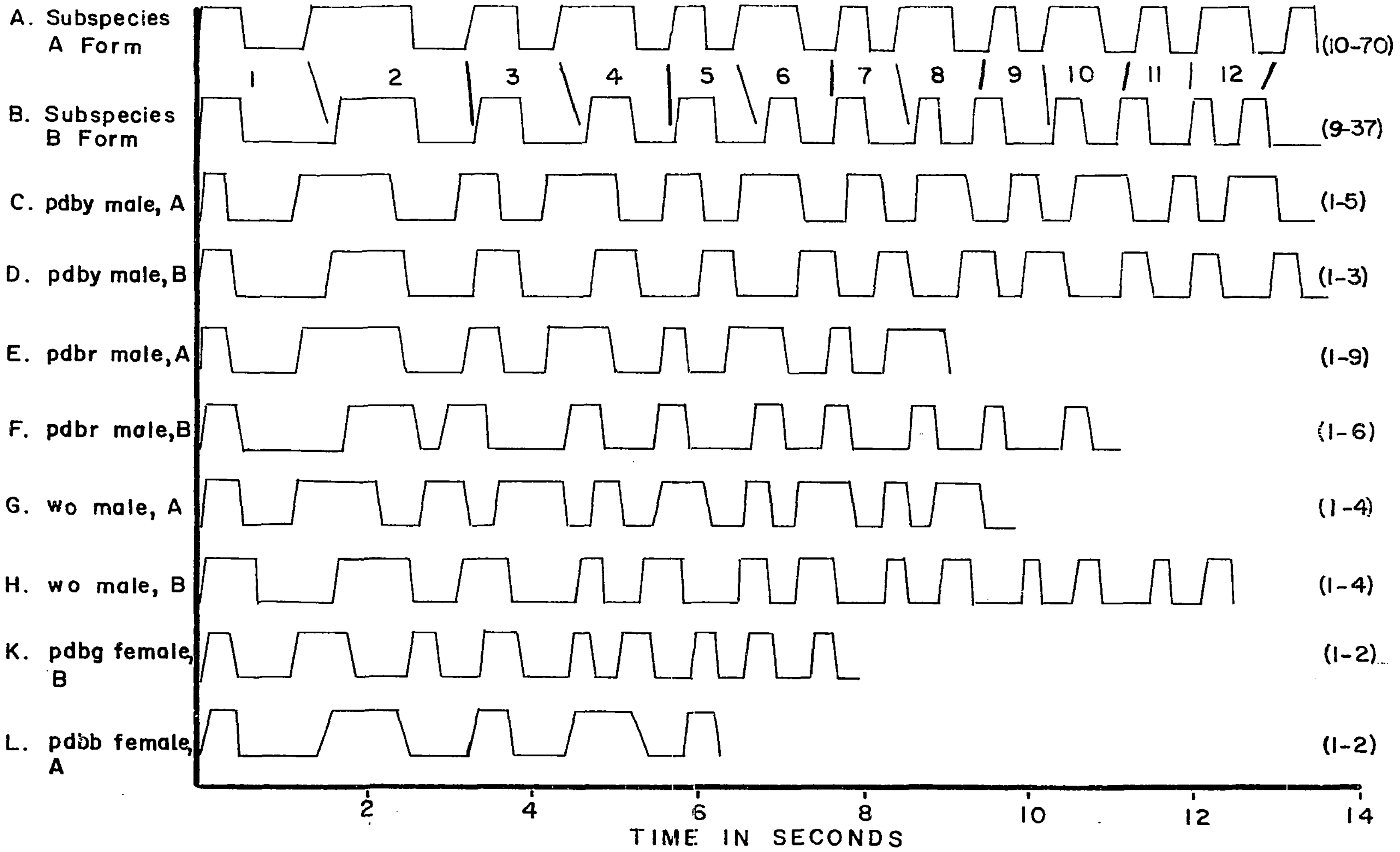

Fig. 9. Display-action-pattern graphs of *Sceloporus h. oligoporus*. See Figure 5 and text for explanation.

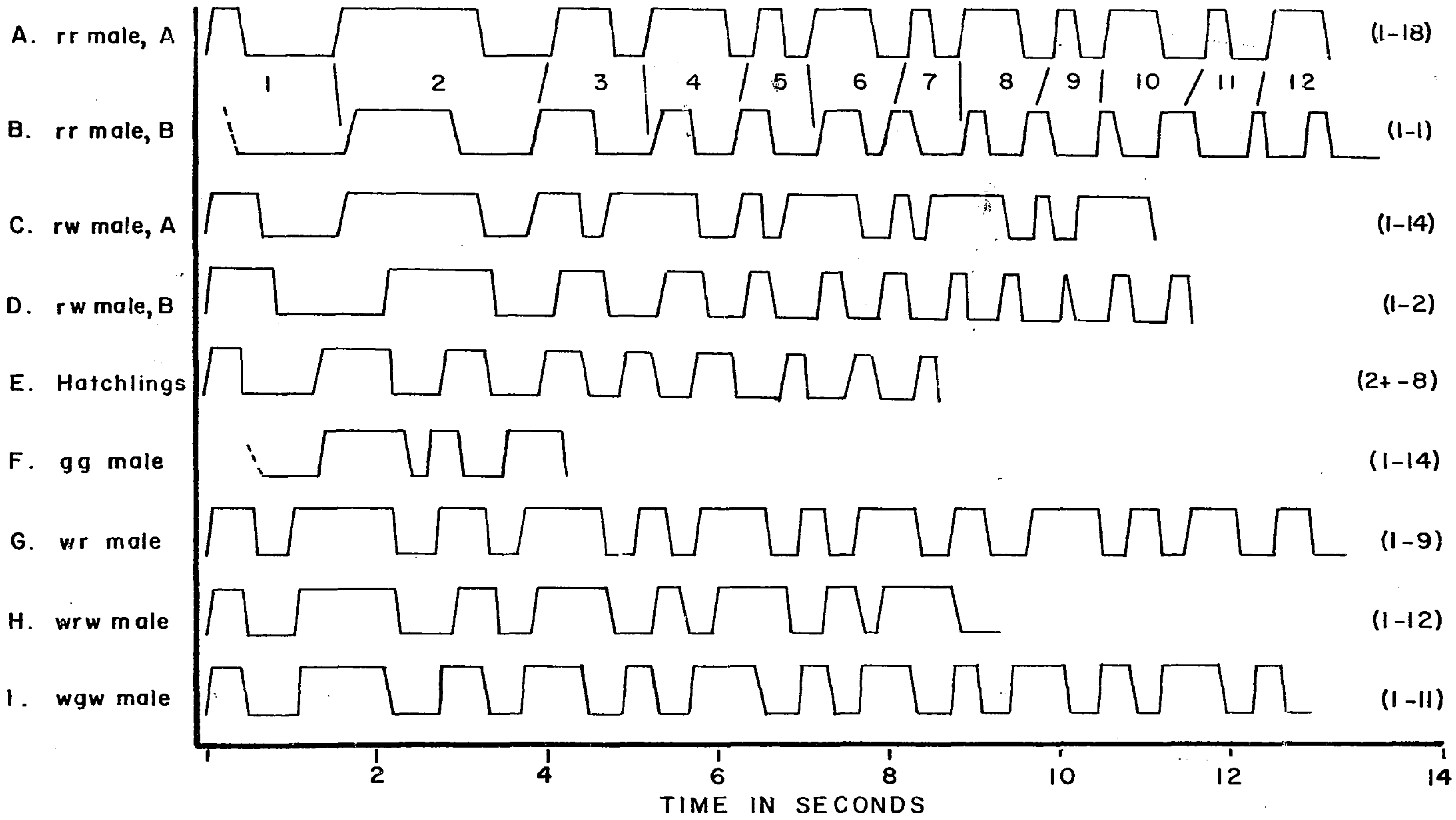

Fig. 10. Display-action-pattern graphs of Sceloporus h. oligoporus from Zihuatanejo, Guerrero, Mexico (A-E) and intergrades of S. h. oligoporus and S. h. albiventris (F-I). See text and Figure 5 for explanation.

and then a repeated pattern of a sharp peaked unit followed by a broader push-up unit (Fig. 7B). Because of the temporal difference in the units, the performing lizard appears to be doing a double unit push-up. In all three patterns, the length of the units decreased as the display proceeded. All the displays of horridus were considered indeterminate in that several forms definitely had three introductory and a repeated set of two units. The A form was considered to be indeterminate from the context of the other forms and because the initial units are much longer than the later ones.

The averaged displays of the two display forms from one female and four males of h. horridus collected near Cuernavaca, Morelos, are presented in Figure 7A and B. The A' and C' forms of the display were actually very similar. The C' display could be derived from the A' display by lengthening the pause of the odd numbered unit while shortening push-up movement of the even numbered unit from the beginning of each unit. Unit 2 only showed a slight reduction, but the even number units, from 4 to 18, showed a marked reduction. These changes greatly affected the appearance of the display even though the total display time remained nearly the same. Two averaged display forms of rg male of 14 units illustrated these changes (Fig. 7E, F). The A' display lasted 14.2 seconds while the C' form laster 14.4 seconds. Grouping the units as pairs, as indicated by the lines, the paired units of the two display forms were shown to be nearly equal after the first paired unit. Male ro showed the same relationship (Fig. 7C, D) as did the other two males. However, when the averaged subspecies displays were determined, the slope of the paired units was changed slightly, but the time relationships remained nearly the same.

An average (MTU) display of h. horridus of the A' form (Fig. 7A) consisted of eight units and laster 11.40 seconds; the averaged C' form of eight units lasted 11.08 seconds which was well within possible measurement error. However, the MTU C' display contained more units and laster longer (14.30 seconds). An eight unit averaged A display lasted 9.55 and 10.35 seconds for h. oligoporus and h. albiventris, respectively. Thus, h. horridus had a slower cadence than the other subspecies. Also, the other two subspecies displays contained fewer units on the average, for the A and B units; h. oligoporus had a MTU of seven for each, while h. albiventris had six and five, respectively. However, this lowering of the MTU was not a subspecific difference, but resulted from their larger sample sizes which included more assertion displays from subordinate individuals.

The most frequently performed display of h. albiventris was the A display (70A, 17B); the MTU A display of six units lasted 8.52 seconds. The relative temporal pattern was the same in all A displays (Fig. 8). Male bwb (Fig. 8) displays were the most variant, but they were only slightly slower in cadence.

The averaged B display (Fig. 8B) differed from the A display by the conversion of the beginning of the even numbered units into the pause of the preceding unit. The relationship of the two forms was indicated by displays of bo male (Fig. 8C, D) and was similar to that described for h. horridus. Only minor temporal variations were observed. An averaged MTU display of five units lasted 8.02 seconds for the B form.

Few challenge displays were observed in h. albiventris. This might be significant or represent the lack of an adequate sample, or, more likely, be the result of no males of this subspecies assuming dominance in the enclosures. It has been hypothesized that the challenge posture functions to present the ventral colored areas to an adversary; these bright ventral blues serving as a "sign stimulus" to inhibit or intimidate the antagonist. Since h. albiventris lacked the ventral coloration, it seemed that there might be a reduction in posturing associated with the display.

Though similar, the displays of h. oligoporus had a slightly faster cadence than those of h. albiventris. However, one population of h. oligoporus from Zihuatenajo, Guerrero, had displays with a slower cadence and they appeared similar to the other two subspecies. This population was midway between sampled localities of h. oligoporus and h. horridus and it seemed as if their displays contained elements of the latter subspecies. Besides performing displays similar to h. horridus, with their slower cadence, rw and rr males were similar in their initial two units in that the form of the later unit pairs was modified almost to the shape of the C' display form of h. horridus (Fig. 7, 10). The averaged display for the A and B variations are depicted in Figure 9. The graphs were based on 70 A and 37 B displays from

13 individuals. Three averaged individual paired displays are presented to show variation in the two forms. Two female displays are presented (Fig. 9); no difference between the sexes was detected. The MTU was seven for both display forms and lasted 8.20 seconds for A and 8.95 seconds for the B form.

Another aspect of the display of h. oligoporus was that it was preceded most often by extra units A and B. Still, they were relatively rare as only 16 of 107 were preceded by at least an A unit (a - .58 seconds, b - .45 seconds). Two also included a B unit (a - .44 seconds, b - .25 seconds). The other subspecies only had three (h. albiventris) and four (h. horridus) A units and no B units.

Displays of several possible intergrade lizards are presented (Fig. 10, F - I). Male gg was obtained from a reptile supply house with a Guadalajara locality (h. oligoporus range), but he had no ventral coloration (as in h. albiventris) (Fig. 10, F). The locality data was considered erroneous and he was called h. albiventris. The other males were collected from a locality midway between known populations of subspecies h. oligoporus and h. albiventris (Fig. 3, Site 12). Because they lacked belly patches, they were initially called h. albiventris. However, since they were collected 6 km from another population in which some males had prominent belly patches (Site 13) and their display patterns, both the A and B forms (Fig. 10, G, H, I) were more similar to those of h. oligoporus, they were considered intergrades.

All previous studies had indicated that the display had very little individual variation. An individual's display was considered to be almost invariant in cadence and pattern, like a person's fingerprint. Differences within an individual's display were rare and considered aberrant. This was true of the U S. forms of the spinosus group of Sceloporus (Bussjaeger, 1967). It was also true of this study although limited data suggested s. spinosus had two fixed patterns. Above the individual level, significant geographical variations have been found in Uta stansburiana (Ferguson, 1969), clarki (Bussjaeger, 1967) and undulatus (Taylor, 1965 and Clarke, pers. comm.). At the individual level, Jenssen (1969) showed the cadence of the displays of male Anolis nebulosus slowed with their being held in captivity (aging). However, Yoshida (1965) did not find any difference due to age in the displays of lizards raised from hatchlings. Therefore, the multiple fixed patterns consistent for both the subspecies and within the individuals was unique for horridus.

Sceloporus melanorhinus

Specimens of melanorhinus were obtained from seven different localities (Appendices I and II). Displays were obtained from only two coastal populations of m. calligaster near Manzanillo, Colima. The localities were separated by 55 km (Fig. 4)

One hundred fifty displays from 19 individuals (14 males, 5 females) were analyzed. The display of melanorhinus was unique for the spinosus group. The display consisted of a pattern of four single units repeated over and over as a sequence (Fig. 11). This type of display pattern is called a "determinate" display by

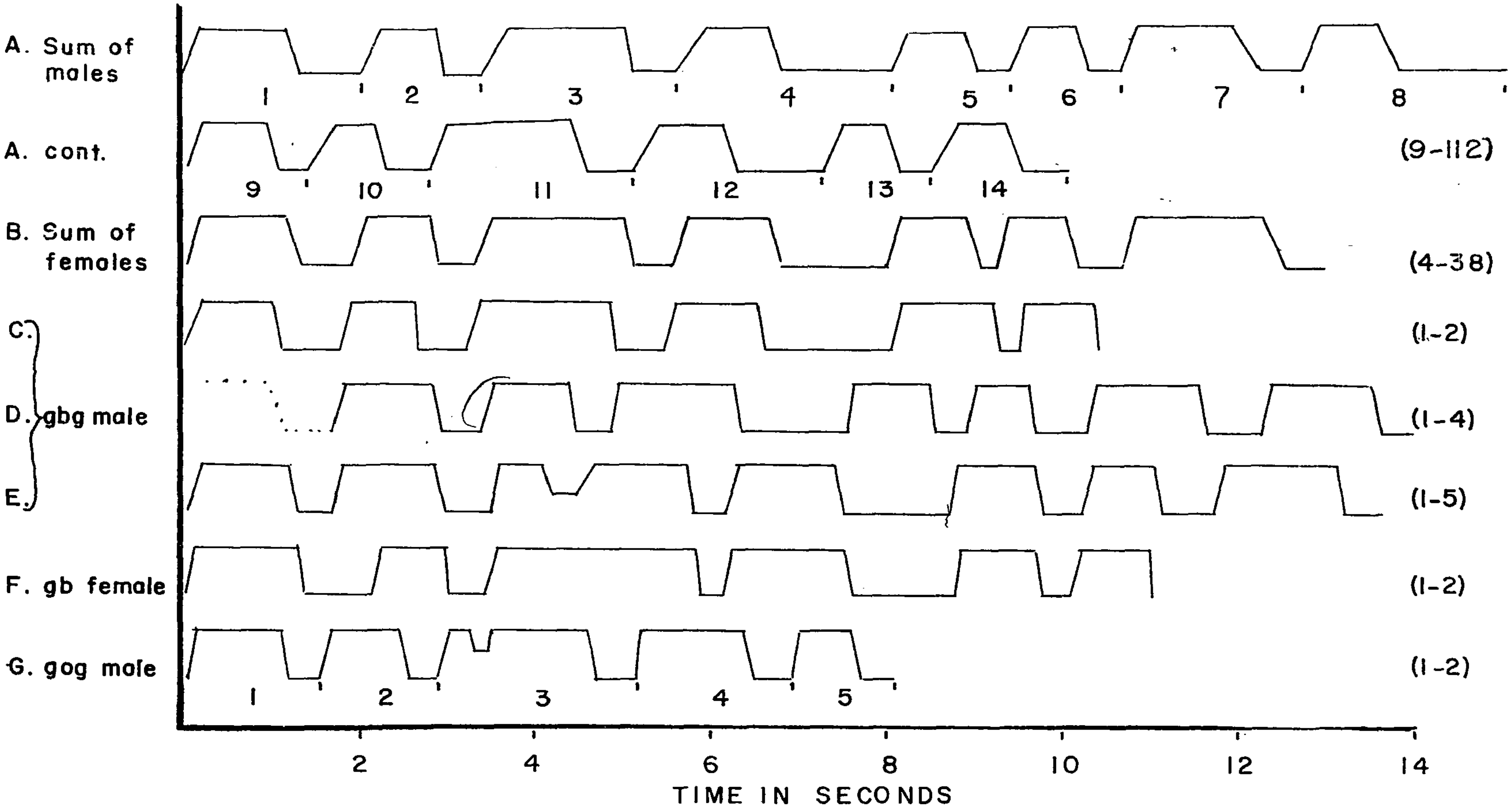

Fig. 11. Display-action-pattern graphs of S. melanorhinus calligaster. See Figure 5 and text for explanation.

Carpenter (pers. comm.). All other spinosus group members performed indeterminate displays.

The four units of the display of melanorhinus formed the repeated pattern of median-short-long (lengthened rise)-long (lengthened pause). The long pause of the fourth unit facilitated recognition of the four unit sequence.

No pattern or cadence difference was observed between the sexes (Fig. 11A, B). There was sexual difference between the number of units composing the complete display. No female performed more than "7b" units while males performed up to "14a" units. Four of the five females ended one-half or more of their displays at the end of unit "2b". The MTU of a typical male display was 6b units lasting 10.80 seconds. Only three males averaged more than 6b units. A female display of four units lasted 8.00 seconds, exactly the same as the males.

The display was defined as beginning with unit number one; but this unit was often (80/150 displays) preceded by unit A, composed of part Aa (peak) and Ab (pause). The inclusion of this unit was highly irregular and Aa was variable in shape. Often it was not a normal up or up-hold-down, but consisted of the lizard rising up and holding the raised position for an indefinite time period. Only 18 of 80 Aa units were similar to a normal push-up unit; they averaged 0.96 seconds for males; no females performed a definite unit Aa.

The A unit might be considered synonomous to the flagging display of Anolis, or stretch display in Callisaurus and Cophosaurus.

It could function in presenting the bright ventral coloration of the male; the females did not perform the _Aa_ unit and they lack the ventral coloration. Thus, the display actually starts in a raised position and begins as a pause (_Ab_) before unit _la_. All males performed at least one display which included the _Aa_ unit.

Aside from the _A_ units, variations in the display were few. The main variation was the form of units 3 and 4. Even the displays of one individual exhibited large variations in these units. The greatest variation was shown by displays of _gbg_ male (Fig. 11C, D, E). Five of 11 displays contained a third unit with the form of a double unit instead of a single (Fig. 11E). The form of the normal third unit of _gbg_ male was variable in length (Fig. 11C, D). Female _gb_ had an extremely long third unit (Fig. 11F), while male _gcg_ also performed a display that included a double third unit (Fig. 11G). The third and fourth units of many of the lizards had inconsistent cadences, but the ratios of the temporal patterns remained approximately equal.

Sceloporus edwardtaylori

Forty-two displays were obtained from nine lizards, of which two were hatchlings. Five individual displays and two averaged displays of this species are presented (Fig. 12). The generalized display of _edwardtaylori_ consisted of a series of single units: two introductory units, the second longer than the first; then a repeated sequence of three single units consisting of a long up and two short up units. Thus, _edwardtaylori_ performed an indeterminant display. Most displays observed were assertion

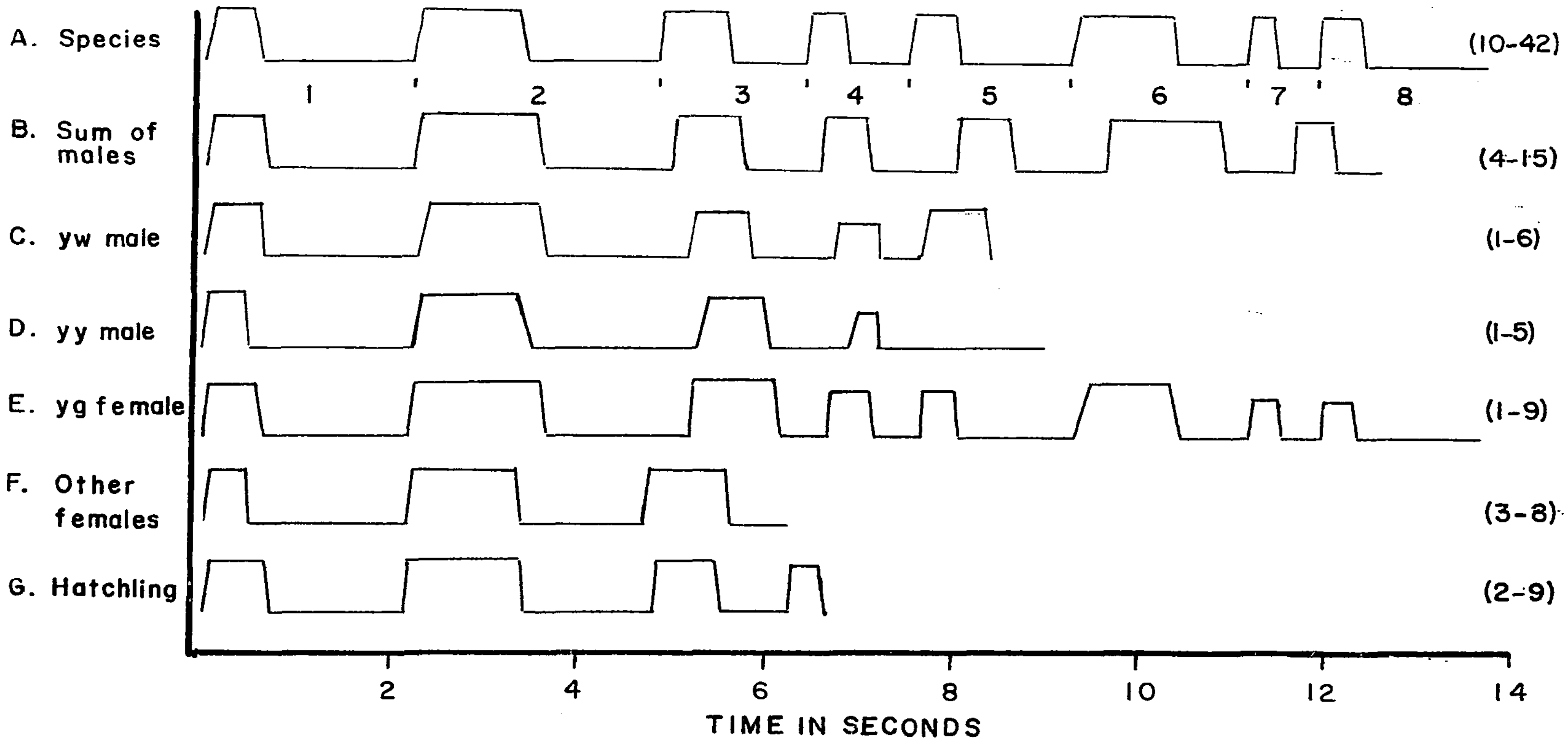

Fig. 12. Display-action-pattern graphs of S. edwardtaylori. See text and Figure 5 for explanation.

displays and contained relatively few units. Only 10/42 displays were longer than four units; of these ten, eight were performed by yg female. She performed one display of ten units; her median display was seven, with a range of three to ten units. The species display was performed at a slow cadence, taking 8.58 seconds for the completion of four units, or 16.24 seconds for 10 units. The MTU of the generalized display was unit three and lasted 6.42 seconds.

Laboratory observed behavior of edwardtaylori was severely inhibited. They did not display at as high an intensity level as observed in the field or as often. Even when kept within the environmental chamber, they did not react normally; however, this was when yg female performed her long displays.

Challenge displays were not observed in adults of this species. However, challenge postures and challenge displays were observed in hatchlings. The postural changes of the young were as pronounced as those seen in adults of other species, with extreme dewlap extension, lateral compression and orientation. The two hatchlings had displays that were identical to the adults even though they were hatched and raised in isolation. Other iguanid and agamid hatchlings have performed the adult display on hatching, indicating the display was an innate species-specific behavior (Yoshida, 1965).

Because this species lacked ventral coloration, one might have expected a reduction in display posturing. Further study is necessary because the lack of posturing might be associated with the limited sample and the apparently aberrant behavior. It was surprising that the young performed these postures readily and the adults did not.

Normally, males perform longer, more vigorous displays than females; this is true of the other spinosus group lizards and all other iguanids studied. The averaged female display was apparently longer than the male display in edwardtaylori (Fig. 12A, B). This resulted from a sampling bias due to excess activity of yg female and to the small sample size. The MTU ending display for all males was unit 4a; for females, unit 3b and more significantly, for all females exclusive of yg female, the MTU was 2a. Thus males had a longer averaged display containing more units than the females, even though yg female was hyperactive and accounted for 10/18 of the female displays. Why this female was so active was unclear. It was not determined if she was gravid, but gravid female iguanids are known to be aggressive and perform vigorous displays, so this might have been the case with yg female.

There were almost no variations found in or between individual displays. Eight individuals were from the same locality; the other, yw male, though collected 55 km away, had an identical display. The lack of variation in the display of edwardtaylori was probably a reflection of the small sample size from a very limited geographic area.

Sceloporus lundelli gaigeae

Four displays were filmed of the one female available. However, another 13 displays were traced, by eye, as she performed them. The display-action-patterns determined from the two methods appear different (Fig. 13A, B). The filmed display consisted of three peaked units (1, 2 and 4), a double unit (3) and a multi-peaked unit of four peaks (5). These four filmed displays were very low intensity assertion displays and contained only 3a, 4a, 4a and 5a units, thus the multiple peaked unit was filmed once. A 5a unit display lasted 4.80 seconds. Of the traced displays, most (ten) consisted of two single units, followed by a double or triple peaked third unit; then a triple peaked unit was repeated twice more. Apparently, the filmed units three and four appeared as one when traced; thus a total of six units were probably observed. Also, the repeated units of the traced display (B) appeared elevated so the peaks did not return to their original level as depicted in A. Variations in the number of peaks per unit was not accurately determined from the traced units. The time scale given for the traced displays was estimated from the comparable filmed units.

Sceloporus cautus

Two males performed eight displays. Their individual and generalized patterns are presented with the generalized olivaceus display from Bussjaeger (1967) (Fig. 13). The display of cautus consisted of a sequence of single units, with units 1-3 progressively increasing in length. Unit 4 was slightly shorter than unit 1. Unit 5 appeared to be a partial unit, but it could be interpreted as a very short terminal unit, as no display lasted longer than 5a units. Only assertion displays were observed in this species as

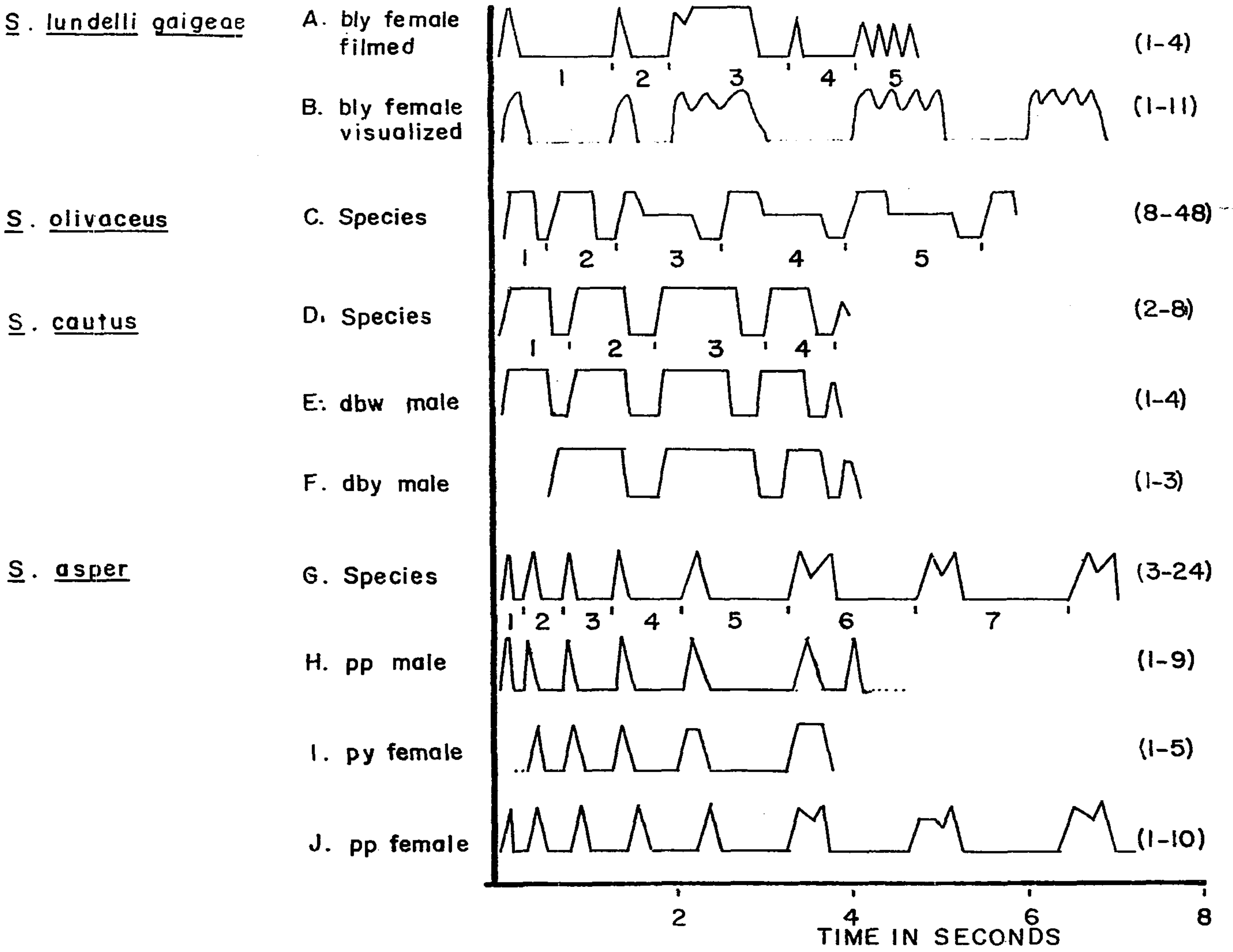

Fig. 13. Display-action-pattern graphs of *S. lundelli gaigeae*, *S. olivaceus*, *S. cautus* and *S. asper*. See Figure 5 and text for explanation.

the two males did not interact. The normal assertion display contained four units (MTU) and lasted 5.61 seconds.

Since the species status of *cautus* was questioned by Hall (pers. comm.), who considered it to be *olivaceus*, it was pertinent to compare their displays. Their displays were very similar in pattern and cadence (Fig. 13, Table 4). However, because of the small sample of *cautus*, this could only be considered suggestive.

Table 4. A comparison of unit times of the displays of *S. olivaceus* and *S. cautus*.

Species	Unit time in seconds					
	1	2	3	4	5	6
olivaceus	.50	.75	1.15	1.50	(.32)*	2.91
cautus	.80	.96	1.26	0.72	(.16)	-
Difference (seconds)	.30	.19	.11	.78	.16	-
% difference from *cautus*	37	20	9	108	100	-

* = only first part of unit; total unit time is 1.58 sec.

The first units were similar between the species in that these units showed progressive increases in time and similar cadences. The first unit was the most variant (37%) of the first three. The pattern of the third unit of *cautus* appeared different but its pattern was one of the variation found in the normal display. The fourth units were quite different; this unit of *cautus* was twice as fast as that of olivaceus. The fifth unit of *cautus* appeared to be a partial unit; thus it seemed to be similar to *olivaceus* in that its terminal unit was also a partial unit.

If these species represent geographic variants of the same species, the differences between their display-action-patterns might be explained on the basis that the arboreal form (*olivaceus*) has a more elaborate display. Lynn (1965) suggested that the reduced displays of *Phrynosoma* were a result of their terrestrial habits.

Besides these similarities, displays of other members of the *undulatus* group of *Sceloporus* (Taylor, 1965) began their display with two similar units followed by a relatively long pause before the third unit which was then followed by a repeated set of two single push-up units. The displays of *cautus* were more similar to the displays of *olivaceus* than to any members of the *undulatus* group.

Sceloporus acanthinus lunaei.

The display of *a. lunaei* was based on 59 displays performed by eight individuals. Two of the eight were obtained near Jutiapa, Guatemala. Four others were collected near the type locality, Salamá, Guatemala; one female of the latter group subsequently gave birth to two young whose displays were also analyzed.

The display was a push-up using the forelegs. Although no challenge displays were observed in the adults, the hatchlings performed many while setting up territories in a terrarium. All the displays were similar and deviated only slightly from the general pattern (Fig. 14B). The display was a combination of single and double peaks. The general pattern was two short single peak and pause units, followed by a third unit which was longer and whose

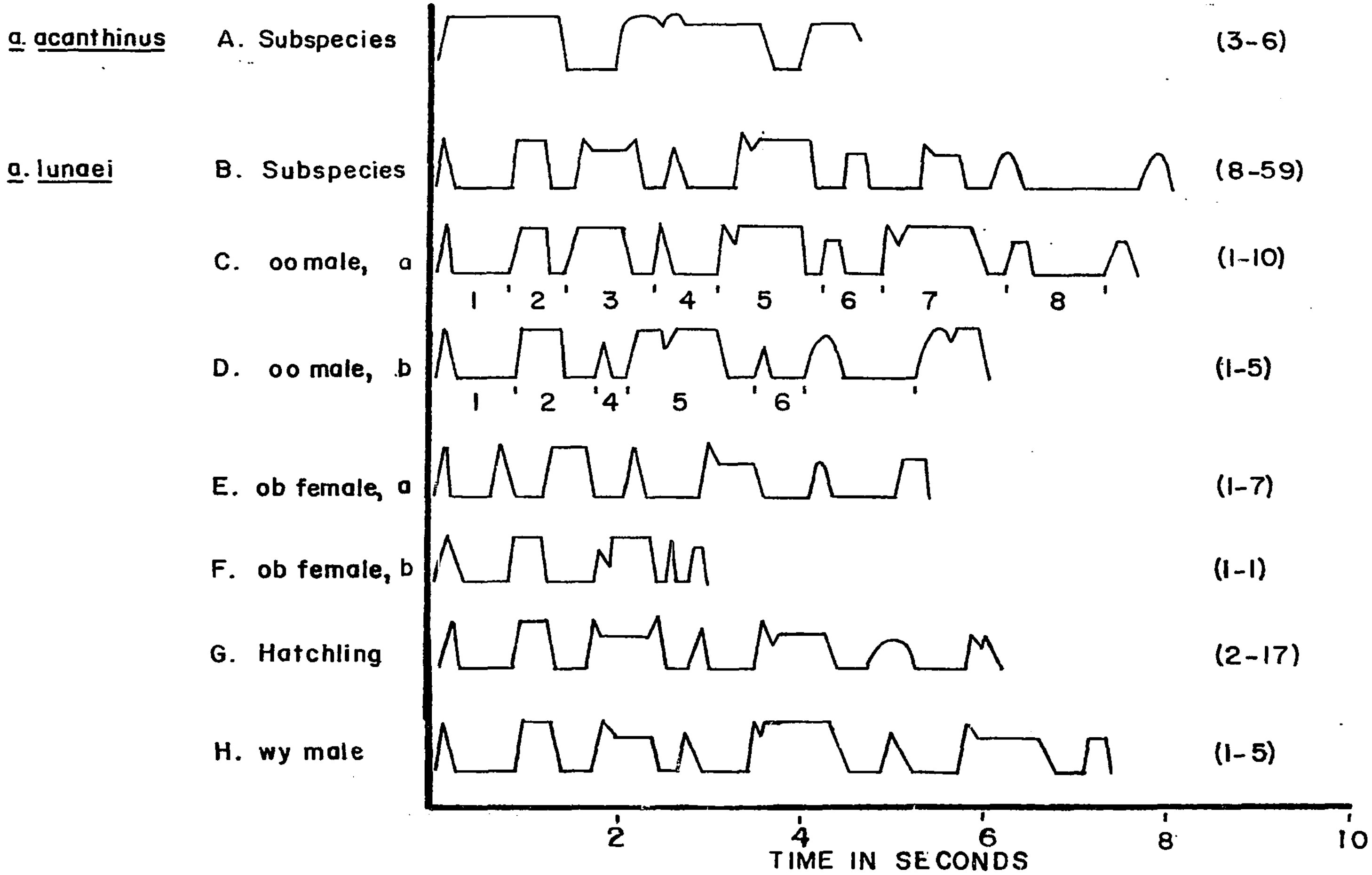

Fig. 14. Display-action-pattern graphs of S. a. acanthinus and S. a. lunaei. See Figure 5 and text for explanation.

form varied. Basically, the third unit was a double peaked unit of a single high long rise with an anterior and posterior peak. Variant patterns included those with no peaks (*oo* male, Fig. 14C), those with only an anterior peak (*wy* male, Fig. 14H), and those who divided the unit into two parts--the first peak lowered to the base line before rising to plateaus (*ob* female, Fig. 14F and *oo* male, Fig. 14D). The fourth unit was a short peak and pause. The fifth unit was similar to the third and was variable also. Usually it was a long single rise with an anterior peak or double unit if the lizard returned to the original base level between peaks. The sixth unit was a short peak similar to the fourth and fifth units. The smoothness depicted in the display-action-pattern graphs (Fig. 14) was not characteristic of the displays of the many individuals especially those units with long raised pauses (units 3, 5, and 7). These pauses were almost always irregular; the peaks of these units represent the most prominent and consistent features of the unit in these generalized displays.

Two lizards performed the major variant displays observed in *a. lunaei*. Male *oo* performed two display patterns (type *a* and *b*); the only individual to do so on a regular basis--the normal generalized display, type *a* and a different display, type *b* (Fig. 14C, D). The latter differed in that two extra units, called 2' and 5' were inserted between units 2 and 3, and 5 and 6, respectively. Those units common to both display patterns were similar in times and patterns; however, the alternate display was longer due to the inclusion of the extra units. Of the 15 displays *oo* male performed, ten were the a pattern, five the b pattern. The displays of ob female were performed at a faster cadence than any other lizard of this species. She performed one type b display.

Sceloporus acanthinus acanthinus

Six displays were performed by three individuals of a. acanthinus. These were assertion displays and contained few (3a) units. The display exhibited a pattern distinct from that of a. lunaei (Fig. 14A). It consisted of two single long up units, the second of which had two anterior peaks. The third unit was a single peak which appeared to be the anterior end of a longer unit, as evidenced by the displaying lizard not returning to the original level. The complete display of 3a units was performed in 4.71 seconds.

Sceloporus asper

The analysis of the displays of asper was based on 24 displays performed by three individuals collected near Tepic, Nayarit (Fig. 13). Only assertion displays were analyzed as challenge displays were not observed. The only postural change observed was a slight dewlap extension by the male. Normal challenge posturing would probably be observed with more males. The display was a rapid push-up and contained two types of units--single-peaked and double-peaked units. The display consisted of a burst of three-peaked units, then a pause which was slightly longer than the pauses separating the peaks. Then came another peaked unit and, after a still longer pause, a push-up movement of either a short hold on a long rise or a double-peaked unit. The sixth unit was repeated, thus the display was an indeterminate display.

Most displays (14/24) contained six or less units; the sixth unit was the median (MTU) as well as the modal unit in which a display terminated (11/24). Eight displays also terminated in units 4 or 5, so 79% of the assertion displays contained 4-6 units (19/24). An averaged six unit display lasted 4.92 seconds.

Because the push-up movements of the display were so rapid, displays were also photographed at 32 frames per second. Some of the apparent differences in the individual display resulted from analyzing the display at too slow a film speed. It was difficult to photograph the beginning of the displays, thus only four first units were photographed, none for <u>py</u> female and only one for <u>pp</u> male. In addition, no complete male display was photographed; four displays containing units 1 to 4a and five displays containing units 4a to 7a were joined to form the averaged male display.

Displays for the three individuals were similar. The major difference was the form of unit six. In <u>pp</u> female, it and the later units were double peaked. In <u>py</u> female, it was a single broad unit and in <u>pp</u> male, it was extremely modified. On the basis of these four displays, the sixth and seventh units of the male could be the same as the divided sixth unit of the female or represent extreme modification of her unit 6.

CHAPTER V

SOCIAL BEHAVIOR

Enclosed populations of lizards have been studied extensively since 1960. In all these studies, the territorial behavior of the males was modified to form a social hierarchy. Social organization of the males ranged from the typical despotic form to a classical peck order or a hierarchy of dominance levels. Female dominance hierarchies have also been noted. Usually, dominance hierarchies were intraspecific while interspecific dominance reactions were between the highest ranking dominant of each species. This resultant social behavior was induced by the space limitations of the enclosure. In effect, the dominant male, by his actions, declared the enclosure to be his territory. Hunsaker and Burrage (1969) hypothesized that a continuum exists between the social behavior and the type of social structure formed between enclosed and natural territorial populations of lizards with the amount of the available space determining the social organization. Enclosing territorial animals to observe their behavior does not change the animals' repertoire of behavior, but shifts the frequencies of different types of behavior action. Such shifts of behavioral activity have been documented in lizards (Carpenter, pers. comm.), baboons (Rowell, 1967) and fish (Ward, 1967).

The social behavior and interactions of four enclosed populations of the spinosus group of Sceloporus were studied. The composition of the species and species groups were primarily determined by their availability. The species, subspecies and sexual composition of the four enclosures with the dates, number of days and hours the groups were observed are listed in Table 2. The two subgroups of the spinosus group of Sceloporus are separated on the basis of dorsal coloration. Since most behavioral interactions tended to follow these lines, this separation should be held in consideration. The striped-back group includes magister, spinosus, horridus and olivaceus; all are terrestrial species except for olivaceus. The uniform back line includes clarki, melanorhinus, edwardtaylori, orcutti and lundelli, and all except orcutti are primarily arboreal.

June 1966 Enclosure

Six species of the spinosus group were observed from 12 June to 29 July in a 5 x 5 m outdoor enclosure at the University of Oklahoma Biological Station, Willis, Oklahoma. Upon introduction to the enclosure, males of clarki and magister formed separate vigorous dominance hierarchies. Besides dominating their own species, the alpha males appeared to dominate (harrass) other species of the spinosus group. For this reason, all males of clarki and magister were removed midway through the study. Their removal did not result in an increase in the activity of the four species which had shown no definite hierarchies: spinosus, olivaceus, cautus and *orcutti*. The lack of increased activity indicated that they were not suppressed, but some other factor was responsible for the lack of activity. Either the population pressure was too great, their behavior was "inhibited" by captivity, or it was too late seasonally for an increase in activity to result. Behavioral interactions normally decrease by midsummer. Except for *olivaceus*, another possible explanation of the lack of activity was the few individuals present of these other species (Table 2).

Three other enclosed populations of lizards were watched during 18 August to 30 September 1968, 2 February to 23 March, 1969 and 21 May to 14 July 1969 at the Animal Behavior Laboratory in Norman, Oklahoma. These are referred to hereafter by the main month of each observation period. Many individuals were observed in all three periods. A short summary of the social structure of each enclosure follows, after which each species is discussed.

August 1968 Enclosure

Prior to the August period, lizards were held indoors for photographic purposes. A dominance hierarchy was probably established in the enclosure prior to the observations because many males had been placed there after being photographed. Three separate species dominance hierarchies were established by males of *melanorhinus*, *spinosus* and *horridus*. No subspecific differences were detected within the subspecies of the latter two species. There was considerable interaction between the two striped species, *horridus* and *spinosus*. *Sceloporus asper* appeared to be a nonentity in the enclosure with respect to the *spinosus* group species as almost no interspecific reactions were observed. Four females of edwardtaylori were present.

In addition to the expected normal male dominance hierarchy, females of horridus and spinosus set up a dominance hierarchy. Several females defended their activity sites from other females and even other males. The vigor of their territoriality was apparently related to their reproductive state as several females were observed to lay small clutches of eggs.

February 1969 Enclosure

Observations were initiated when males were noticed becoming extremely active in the enclosure. This enclosed population was established in the fall of 1968, but, by February, mortality had reduced it to predominantely two species: spinosus and horridus.

Activity was characterized by intense aggressive interactions among the males of horridus. Males of spinosus were generally inactive and appeared to be subordinated as well as wary. Females, in contrast to the August observations, were inactive and most of their social activity was courtship rejection behavior.

June 1969 Enclosure

The lizards remaining from the February observation period were observed along with the formosus group individuals, acanthinus, and additional members of the spinosus group: magister, lundelli, and melanorhinus (Table 2). Social structures were determined for the males of four species: horridus, spinosus, magister and acanthinus. As in the preceding August, females of spinosus and horridus were aggressive and defended individual sites inter- and intraspecifically.

Species Accounts

In each species, or species pair account, a brief summary of inter- and intraspecific encounters--both sexual and aggressive--are given. Where applicable, a social status chart of dominance encounters, courtships and number of displays performed are presented. Finally, the overall implications are discussed.

Sequential Dominant Removal, June 1966

Dominant males of clarki and magister were removed sequentially on 28 June, 1 July and 6 July (Table 5). One index of dominance was the total number of displays performed (Griffith, 1966). The dominant performed the most displays; subordinant males performed relatively few displays. When the dominant was removed, a dominance shift occurred with a subordinant assuming dominance as evidenced by his increased activity. Which subordinant would become dominant could be predicted on the basis of his previous activity as a subdominant. In both species, the second dominant male showed the most dramatic increase in activity on assuming dominance. Those lower ranking subordinants were less active as dominants when they finally assumed dominance. This lowered activity could be due partially to there being fewer males with which to interact, but the slow assumption of dominance by the lowest ranking subordinant male seemed to be related more to his position in the original hierarchy as the last dominant magister performed more displays than the

Table 5. Total displays (push-up and courtship) performed by males of *S. clarki* and *S. magister* from 14 June to 9 July, 1966. Males listed in order of sequential dominance. Dominants removed after last date indicated. Underline indicates period of dominance.

	Male	Date															Hours observed as dominant
		June										July					
		14	15	18	20	21	22	24	28	29	1 am	1 pm	2	5	6	8	
magister	ww	8	44	11	22	44	54	48	45								24.5
	wr	1	2	0	5	11	7	18	2	70	73						6
	wo	2	6	5	0	20	9	10	7	2	1	1	1	10	5**		4.5
	wg	0	2	0	0	7	0	8	2	8	0	0	0	2	7	23	5
	wy	3	11	1	*												
clarki	ry	42	82	38	17	51	27	60	49								24.5
	rlb	0	0	0	0	3	0	5	4	102	57						6
	rr	0	4	0	0	1	0	0	1	4	0	25	48	20			4.5
	rw	18	2	1	1	7	5	5	0	16	1	4	3	0	0	14	5
	ryr	1	5	0	0	0	0	0	1	1	1	0	0	0	2	6	0
	rg	0	2	1	0	3	0	0	0	0	0	0	0	0	2	0	0
	rylb	1	0	1	0	0	2	4	2	2	0	0	0	0	0	0	0
	Hours observed	4	5	2	1	4.5	3	3	2	3.5	2.5	1	1.5	2	3	2	

* found dead.

** removed that day before wg male became active.

corresponding dominant clarki, though four individuals of the latter species were present (Table 5).

Actually, dominance hierarchies result from and are recognized from interactions between males. This was the basis for the prediction of future dominants. For example, in clarki, male rlb was very inactive compared to rw male in the number of displays performed while they were subordinants (Table 5). But, during this period, rlb male won three dominance encounters over rw male. On this basis, he was accurately predicted to be the next dominant. Thus, agonistic encounters are predictive of dominance while display activities are a result or parameter of dominance.

Although similar, there was a noticeable behavioral difference between clarki and magister. Males of clarki remained active, in view, much longer and more often than males of magister. This resulted in a stronger despotic hierarchy being formed by clarki, as the dominant was present and reinforced his dominance more often. The males of clarki were more subordinant than equal ranking males of magister. For example, until the original dominant was removed, the three highest subordinant males of clarki performed 52 displays compared to 134 performed by subordinants of magister. The greater activity was considered a result of the more flexible behavior of magister which resulted from what I called "presence dominance." Unless a higher ranking male was present and visible, a subordinant would act like a dominant--chasing lower subordinants, displaying and courting. When a higher ranking male appeared, the lower ranking male would flee. Although not as pronounced, this same relationship was previously seen in magister by Bussjaeger (1967). This relationship is supported by field observations; magister (terrestrial) is much more wary than clarki (arboreal) (Smith, 1946).

When aggressive encounters were observed, the lizards were scored as dominant (winner) or subordinant (loser). The dominant either chased, won a fight or caused the other male to either freeze, flee, avoid or adopt a submissive posture. In addition, if a male "courted" (performed a rapid head nod to another male), the recipient was scored as a subordinant. This latter behavior was observed most often in interspecific encounters and may signify incorrect sex recognition. The intraspecific dominance interactions formed a straight line dominance hierarchy for the sequential dominants. Specifically, no male defeated a higher ranking male of his own species (Table 6). Each male was most active, as evidenced by the number of displays performed (Table 5), and encounters won (Table 6) during his period of dominance. This is even more significant if one considers the total time each of the original three subordinants was active as a dominant which was only 12-20% of the total observed time (Table 6).

One weak interspecific encounter was observed; a dominant magister appeared to cause a subordinant clarki to flee. The males did interact in a type of social facilitation (allelomimetic behavior). When the dominant of one species displayed, the other dominant also displayed and often they appeared to orient towards one another while displaying.

Table 6. Intraspecific aggressive encounters won during respective periods of dominance of the four sequential dominant males of S. clarki and S. magister, Summer, 1966

	S. magister				S. clarki			
	ww	wr	wo	wg	ry	rlb	rr	rw
Total encounters won	31	22	3	0*	73	42	8	8
Number won as dominant	31	16	2	0	72	34	5	2**
Percent won as dominant	100	73	67	0	100	81	62	25
Percent of total observed time spent as dominant	100	20	13	12	100	20	13	12

*only magister in pen during his dominance period.
**won three of the six other encounters during periods of dominance shifts.

When these dominants were removed to another enclosure with fewer lizards, they were observed in interspecific fights with each other. Bussjaeger (1967) observed interspecific encounters between dominant magister and clarki with the latter winning 10 of 11 interspecific encounters (out of a total of 178 agonistic encounters). These 11 interactions occurred late in the observation period after intraspecific dominance hierarchies had been established.

Sceloporus clarki

At least two populations of clarki were represented in June 1966: c. boulengeri from Sinaloa, Mexico, and several clarki from a supply house in Arizona. They did not initiate any reactions with magister and apparently recognized magister as a different species. However, the three allopatric species had about the same rate of interaction with clarki as was observed with magister

(Table 7), but they were statistically significantly different from random interactions. The encounters of *clarki* with *olivaceus* were more vigorous than seen in *magister*; still 50% of the encounters were simply avoidances of *clarki* by *olivaceus*. Also, as in *magister*, *clarki* interacted with *s*. *spinosus* at a higher percentage than expected on the basis of available interspecific males. These reactions were vigorous encounters and might indicate that the males were treated like conspecifics.

Table 7. Interspecific dominance encounters initiated by *S*. *magister* and *S*. *clarki*, June 1966.

		Dominant			
		magister		*clarki*	
Species of *Sceloporus*	Total Males	No. of encounters observed	expected	No. of encounters observed	expected
olivaceus	18	14	15	29	23
spinosus	3	5	2	8	4
orcutti	5	7	4	3	7
clarki	7	1	6	(133)*	-
magister	5	(55)*	-	0	6
Total encounters		82		173	
% interspecific encounters		31.2		24.4	
level of statistical significance for random interactions		.05		.01	

*intraspecific encounters

Sceloporus clarki was involved in 76 courtships, of which 21 (27.4%) were interspecific. Of these interspecific courtships, 16 were to females of olivaceus, three to females of spinosus, and two to females of orcutti. Each dominant performed most of his courtships during his period of dominance.

In the June 1969 enclosure, one male c. boulengeri was available. He interacted with males of acanthinus, horridus and spinosus and with females of the latter two (Table 15). Most females of the spinosus group of Sceloporus have similar color patterns. Hence, the courting of an "incorrect" female is understandable in enclosures lacking conspecifics. In dominance encounters, clarki interacted more often with acanthinus and spinosus. Instead of this showing a preference for these two species, I feel the male clarki demonstrated a recognition of sympatric horridus, thus selecting against horridus rather than for acanthinus and spinosus.

Sceloporus magister

Intraspecific encounters occurred at a much higher frequency than expected if males of all species interacted at random (Table 7). Yet, males of magister interacted with a relatively large number, 27 (31.2%), of males of other species. Even these interspecific differences did not appear to be at random, although the sample was small, because the interactions were statistically significant. This differential species interaction seemed to be caused by magister recognizing clarki; if the data are recalculated without clarki, the males of magister reacted with the other species at random. The difference may correlate with clarki being the only species sympatric with magister. The higher number of interactions with orcutti was probably a result of its being allopatric since this subspecies(o. tortugensis) was an insular form with basic coloration similar to magister females. Five of seven interactions between these males were "courtship" rapid head nods. It seems as if the males of magister accepted the smaller males of o. tortugensis for females. Most interspecific interactions seemed weaker than intraspecific interactions. As no females of magister were present in June 1966, males of this species performed five interspecific courtships towards females of: clarki (1), orcutti (2) and spinosus (2).

Only four magister were available in the June 1969 enclosure. A male and female were placed in the enclosure on 4 June and two males were added on 12 June. The first male established and maintained dominance in the enclosure. He had extensive fights with the similar-sized male, but the smaller male was not challenged.

Although magister was present with a number of species, the intraspecific interactions and courtships were higher than expected on basis of the number of available individuals. Males of magister appeared to be quite discriminate, interacting primarily with members of their own species (Table 8). Interspecifically, magister males courted other females randomly and failed to interact with the other males. Possibly one reason for not interacting was that males of spinosus and horridus were larger while males of acanthinus were smaller.

Table 8. Social interactions of S. magister males, June 1969 enclosure.

Species of Sceloporus	Dominance Available males	Dominance Numbers Encounters	Courtships Available females	Courtships Number Encounters
magister	3	22	1	30
spinosus	4	4	7	10
horridus	6	0	10	16
acanthinus	5	0	7	10
lundelli	0	-	1	2

Sceloporus olivaceus

A loose dominance hierarchy was formed by the enclosed male population during June 1966. No male was a despot, suppressing the activities of the other males. This social status was indicated by the similar number of aggressive displays and courtships performed (Table 9). However, one male, olbo, acted as if he would assume dominance during the initial period of the study. He performed 128 aggressive displays, 10 intraspecific courtships and won 11 intraspecific dominance encounters, losing none. Except for not suppressing the activity of the other male olivaceus, he acted like a dominant. He lost seven interspecific encounters to males of clarki and magister (Table 9). A total of 43 encounters were lost to these two species by male olivaceus. This subordination to other species may have prevented a strong dominance hierarchy from arising within olivaceus. However, the removal of these species

Table 9. Dominance encounters, total displays and courtships performed by males of *S. olivaceus*, June 1966 enclosure.

		Dominance Winners and Courting Males													
		olivaceus										other *Sceloporus*			
		olbo	oro	ogo	owy	oyo	owlb	owg	owr	other	Tot	*cl*.	*ma*.	*or*.	Tot
losing males *olivaceus*	olbo	-									0	3	4		7
	oro	2	-				1				3	5	2	1	8
	ogo	1	1	-	1						3	2	2		4
	owy	1		3	-						4	5			5
	oyo					-					0	1			1
	owlb	1		1		1	-				3	4			4
	owg		1					-			1	1			1
	owr	2	1				1	1	-		5	2	1		3
	other	4	3		2					1	11	6	5	1	12
Subtotal		11	6	4	3	1	2	1	0	1	33	29	14	2	45
Interspecific				1		1		1		3	6				
Total		11	6	5	3	2	2	2	0	4	39				
courtships	*olivaceus* females	10	2	2	1	4	4	4	5	3	35	7			7
	other females	3							1		4				
	Total	13	2	2	1	4	4	4	6	3	39				
Total Displays		133	73	72	31	42	24	18	85	87	583				

did not result in the formation of a dominance hierarchy. In fact, the number of displays performed and encounters dropped below the level observed while these two species were present. In other species, interspecific dominance interactions have not disturbed intraspecific social behavior.

The males of olivaceus are ranked in Table 9 according to their apparent order of dominance on the basis of dominance encounters. Two encounters were observed in which a subordinate won an encounter with a higher ranking male, but all encounters established the dominance rankings presented here. Such apparent inconsistencies in the dominance sociograms are normal reflections of the dynamic state of the behavioral interactions. The sociogram depicts the static total and does not depict the changing relationships between males. Higher ranking lizards tended to display more often; owr male was an exception. He was a small active male who displayed often, but was generally not challenged by the larger males. This and other data indicated that different size classes of lizards do not interact (Rand, 1967; Hunsaker and Burrage, 1969). The low ranking of owr male resulted from his losing all his dominance encounters. The highest ranking male, olbo, performed the most courtships, but the next ranking males performed fewer courtships than the lower ranked males.

Compared to males of clarki and magister, olivaceus was inactive. The activity of olivaceus males was not much greater than that of the females; 14 females performed 358 displays while 17 males performed 583 displays. Three of the seven lizards which performed the most displays were females. Blair (1960) stated that olivaceus laid up to four clutches of eggs per season in Austin, Texas. These, taken from Fort Worth, laid several clutches near the end of June. Therefore, it seemed that the males should have been strongly territorial since it was the middle of their breeding season.

Female displays included push-ups (297) and rejection display (62); the latter was the irregular lunging and hopping the females do while assuming a rejection posture in response to a courting or approaching male. The rejection display was the same as described for undulatus by Carpenter (1962a). The displays consists of the female arching her back, bloating her trunk region, rising on four legs and orienting the up-curved tail caudally towards the courting lizard and then performing a series of lunges or sidle-hops. The one significant difference was that females of olivaceus performed the display to non-courting males and to females, sometimes when they merely passed nearby.

Males of olivaceus performed this rejection display, also. This was unusual in that the males seemed to have adapted a female display to their own use. This has been observed before in young Uta (Carpenter, pers. comm.). In males, the display seems to have a neutral or subordinate function. Some males performed this display when a dominant male approached, displayed nearby or otherwise threatened them. Never did a male in rejection posture take the offensive, and often he was chased by the male towards which he displayed. Thus, both sexes use the rejection display; the females to fend off courting males of *olivaceus* and males of *olivaceus* to appease challenging males.

The lack of male aggression in *olivaceus* might have been due to overcrowding, to subordination to other species, or to increased female aggression. Since normally only one sexual pair is found per tree (Blair, 1960), one might expect a higher level of aggression in the females--approaching that found in males. The high number of female displays and the readiness with which they performed the rejection posture in non-courting situations tends to support the hypothesis of increased female aggression. The fact that males perform the female rejection posture as a subordinate display seems to indicate lower levels of male aggression.

Sceloporus olivaceus males showed a high degree of species specificity by courting their own females in 35 of 39 observed courtships. A dominant male was responsible for three of the four interspecific courtships of *clarki* females. Males of *clarki* courted female *olivaceus* six times. No courtships resulted in copulation.

Sceloporus melanorhinus

August 1968, was the only observation period in which a population of *melanorhinus* was available. A weak dominance hierarchy was established by the males (Table 10). The primary expression of the weakness was that the males of *melanorhinus* were relatively inactive. A total of only 77 displays, 38 dominance encounters and 6 courtship attempts were observed. This activity level was two to ten times less than observed in the striped-back members

Table 10. Dominance encounters, courtships and total displays performed by males of S. melanorhinus, August 1968 enclosure.

		Dominance winner and courting males									
		melanorhinus								Other Sceloporus	
		gy	grg	go	gwg	gyg	gr	gb	gbg	horridus	spinosus
subordinant males melanorhinus	gy	-									
	grg	4	-								
	go	7	1	-	1						
	gwg	3	2	3	-					1	
	gyg	3				-					
	gr	3	3	1			-				
	gb	2	2		1		1	-			
	gbg					1					
	g?		2								
horridus			1								
spinosus			4								
Total encounters		22	15	4	2	1	1	0	0	1	
courted females ed. melan.	gy		3					1			1
	gw		1								
	yg		1								
	Total		5					1			1
Total No. of Displays		25	30	0	4	3	2	1	1		

of the spinosus group in this same enclosure. For most of the observation period, two males appeared established as co-dominants and interactions were not observed between them until late in this period.

Social interactions in this species were an intermittent activity; a subordinant almost had to approach the dominant to elicit a dominant response. Active patrolling of the enclosure and suppressing subordinant lizards did not occur. Most encounters occurred on the posts and trees. Though few dominance interactions were observed, the activity level of the subordinants was low. They acted as if they were subordinated at the same intensity as observed in the striped back forms. For example, on their first day of introduction, two males, grg and go, were active and seemed equally dominant. On the following day, gy male appeared to have displaced go male and the latter was never active again. Males grg and gy acted as codominants. This was apparently facilitated by the separate tree-like objects in the enclosure as they occupied different alert sites. Midway through this period, gy male was observed to win several encounters over grg male. However, grg male continued to court and subordinate other lizards. Overall, male gy won all 21 intraspecific encounters while grg male won ten encounters with other males, losing four to gy male. These two males performed 55 of 66 observed male displays and performed five of six observed courtship attempts (Table 10). Five of the six courtship attempts were intraspecific and the one interspecific courtship was to another uniform back female, edwardtaylori.

Sceloporus melanorhinus was involved in very few interspecific interactions. Males of *melanorhinus* challenge postured to males of *spinosus* (four) and *horridus* (one) and once a male *melanorhinus* was chased by a male *horridus*. Thus, *melanorhinus* interacted weakly with the two striped forms of the *spinosus* group, which seemed to indicate their ability to distinguish their own kind.

Sceloporus asper

Three individuals, one male, were present in August 1968. This arboreal species spent most of its time on the tree-simulating forms. No courtship behavior was observed; the male performed 20 assertion displays while the two females performed six displays. Numerically, the male performed an equivalent number of displays to those performed by the dominant males of *melanorhinus* (25 and 30). The low number of displays could be the result of only one male being in the enclosure, or its being "inhibited" by the larger sized and more numerous members of the *spinosus* group, or it could be representative of the general lack of activity seen in other arboreal species. *Sceloporus asper* was not involved in any interspecific encounters. They seemed to be a social non-entity in the enclosure as the other species appeared to ignore them.

Sceloporus horridus and Sceloporus spinosus

Sceloporus horridus exhibited typical, active, iguanid social structures as reported for other species (Carpenter, 1967). Besides establishing an intraspecific peck order, they interacted with *spinosus*. When observations began in August, two males, *rr* and *rw* were active. Because no interactions were first observed between them, they appeared to be temporal dominants, active at different time periods. After four days, rw male established himself as dominant as indicated by the greater number of encounters won, displays performed and courtships initiated (Table 11). The loss of dominance by rr male may have been accelerated by the introduction of spinosus male ywb.

Initially, the males of spinosus were relatively inactive; one, wo male, exhibited dominance tendencies (Table 11). However, when ywb male was introduced into the enclosure, he assumed dominance, defeating wo male and males of both horridus and spinosus. The only exception was then dominant rw male horridus who lost an encounter, but was not subordinated by ywb male (Table 11). Except for the small males, each dominant suppressed completely those males of his species, but interaction between the species did not result in subordination of the other males (Table 11).

In the latter part of this observation period, the male hierarchy of spinosus dissipated. Apparently this resulted from ywb male losing dominance in a fight with ww male. Neither combatant assumed dominance but with the removal of the dominant rw horridus, wg male spinosus became active. He performed 11 of his 13 push-up displays in this period. Because he was not observed to interact with other spinosus, his dominance status could not be determined.

In the 42 hours (18 days) the enclosure was under observation, males of spinosus and horridus were observed in 191 encounters--104 intraspecific, 60 interspecific, and 27 in which

Table 11. Dominance encounters, total displays and courtships performed by *S. horridus* and *S. spinosus*, August 1968 enclosure.

		Dominance Winners and Courting Males															
		horridus										spinosus					
		rw	rr	br	rb	rg	pdby	pdbo	ro	ryr	other	wo	ywb	wg	ywo	wb	other
Losing males, horridus	rw	-	1														
	rr		-										2	1			
	br	5	4	-									2				
	rb				-								2				
	rg	4			1	-											
	pdby	2	1	2			-					2					
	pdbo	6	2					-					1				
	ro	1			1			1	-								
	ryr	5	1							-		1	1				
	other	44	2	1	2	1	4	2	2	1	-	0	15	1	1	2	
Total		167	11	3	2	1	4	2	2	1		3	23	2	1	2	
Losing males, spinosus	wo	8										-	1				
	ywb	5											-				
	wg	1	1											-			
	ywo	4						1				1	1		-		
	wb	1										2				-	
	other	4					1					5	3				
Total		26	1				1	1				8	5				
Unknowns		5	2					1	2			3	13		2		
Females, courtships	Intra	18	1	2	5		1	1			6		4				1
	Inter	10	5	2	2		1				1	1	3			1	1
	Unknown	4	2	2							1						
Total		32	8	6	7		2	1			8	1	7			1	2
Total Displays		592	172	27	10	5	27	12	2	3	77	104	38	12	29	5	18

one of the participants was unidentified. If one considers the interactions in which the recipients were identified, it appeared that males of _horridus_ showed a decided preference for their own species, while _spinosus_ did not (Table 12). This conclusion is probably erroneous; considering the numbers of each species available for interaction, one would expect a species preference of 2:1 in favor of _horridus_ if there were a lack of species recognition. Furthermore, two factors should increase the interactions of _horridus_ males: they were more active and less skittish.

Table 12. Social interaction between _S_. _horridus_ and _S_. _spinosus_ August 1968 enclosure.

		(n)*	Dominant male _horridus_ (19)	 _spinosus_ (10)
Subordinant male:				
	horridus	(19)	91	29
	spinosus	(10)	31	13
Female courted:				
	horridus	(19)	31	4
	spinosus	(9)	21	5

(n)*number of each sex in enclosure.

Even more illuminating were the 61 courtships observed between the two species (Table 12) As mentioned above, there were unequal numbers of the two species but the males courted females of both species almost equally. In fact, on the basis of females available, it would seem that both species preferred to court _spinosus_ females. However, unlike the males, females of _spinosus_ were in view more often than horridus females and thus more available for courtship.

Since these two species are similar morphologically and have allopatric distributions, one would not expect strong effective isolating mechanisms to be found. From the data, it is apparent that this was true. Table 12 shows that the males did not restrict their interactions to their own species, but interacted as one would expect on the basis of chance.

In the February 1969 period, few interactions were noted between males of spinosus. One male, wg, assumed dominance by being the most active male and subordinating three other males (Table 13). However, compared to the males of horridus, they were very inactive and the species seemed subordinated by horridus. The initial dominant horridus was rw male, the dominant of the previous August period. A dominance shift occurred and ryr male replaced rw male as the dominant. Male ryr remained dominant until removed on 18 February; then rw male reassumed dominance. Male rw was present for the entire observation period while male ryr was present only three-fourths of the time. But, since their periods of dominance were mutually exclusive, this accounts for the high degree of display, dominance and courtship activity of both males (Table 13).

Male ryr was a hyperdominant. He actively suppressed any similar sized male horridus. On seeing a male, he would display or chase the lizard vigorously. If the subordinant male

Table 13. Dominance encounters, number of displays and courtships performed by *S. horridus* and *S. spinosus* males in February 1969 enclosure.

		Dominance Winners and Courting Males															
		horridus									spinosus						
		ryr	rw	bwb	rb	ro	bo	rg	pdbo	rr	wg	ywb	wr	ywy	wb	byb	ww
Losing Males — horridus	ryr	-	4		1												
	rw	33	-	2			1				2				1		
	bwb	22	8	-													
	rb	18	3	1	-												
	ro	31	15	1	1	-											
	bo	11	13	8			-										
	rg	34	5	4	2	3		-				2					
	pdbo	6	6			1			-								
	rr	5								-							
Total		162	54	16	4	4	1	0	0	0	2	2			1		
spinosus	wg			1				1			-						
	ywb	1		1							4	-	1				
	wr	4									2	1	-	1			
	ywy	3	4	1					1				1	-			
	wb										2				-		
	byb															-	
	ww																-
Total		8	4	3				1	1		8	1	2	1			
Females courted	*h. horridus*	41	33	9		1	9	1	2							2	1
	spinosus	10	10	1								1					
	edward.	2	2		0	2			2								
	other	3	13	1			1										
Total		56	48	11		3	10	1	4			1				2	1
Total Displays		424	337	84	4	7	35	2	49		19	6	5	5	3	1	0

adopted a submissive posture--a motionless prostrate position on the sand--which normally prevents further attacks by the dominant male (Carpenter, 1962a), ryr male would attack the prostrate male until it fled. Typically, male ryr approached the male, challenge-postured, challenge-displayed; then he would sidle into and tail-slap or bite the male until he fled. Chases by the male would last five minutes or more. Subordinates would flee on seeing ryr male, even though he was motionless; often while fleeing from him, they would run head-long into the enclosure wall. Once, a subordinant male fled into and remained submerged in the water bowl--a behavioral pattern of another iguanid, Basiliscus. This same reaction has been observed in a female horridus attempting to escape from me.

One male horridus, bwb, was active during the dominance of ryr male. This male was smaller (86 mm) than ryr male (95 mm) and apparently this size difference allowed bwb male to be active. Male bwb displayed and dominated other males of horridus in the presence of ryr male. If a male responded to bwb male in ryr male's view, male ryr male would chase the recipient of bwb male's action.

Clearly, males of horridus were more active than spinosus (942 displays to 39 displays). Most (27/39) of the displays of spinosus were performed during a horridus dominance shift. The exact correlation of these two phenomena is unknown; it is probably correlated to the increase in the activity of several males of horridus.

In this period, these two species acted as separate species with very little interspecific interaction (Table 14). Males of both species apparently recognized each other. Males of horridus showed a significant preference for females of their species. The males of spinosus appeared to court at random. This switch from a lack of species recognition in the fall to the high degree of species specificity in the spring seemed to indicate a seasonal change in species recognition.

Table 14. Social interactions between S. horridus and S. spinosus, February 1969 enclosure.

	(n)*	Dominant male horridus (8)	 spinosus (7)
Subordinant male:			
horridus	(8)	233	5
spinosus	(7)	14	12
Female courted:			
horridus	(14)	103	22
spinosus	(8)	3	1

(n)*number of each sex in enclosure.

In the suceeding observation period, June 1969, the interrelationship between males of spinosus and horridus was demonstrated further. One male, ro, horridus, assumed dominance in the enclosure after an initial conflict with February dominant, ryr male. Male wb was the active dominant spinosus (Table 15).

Table 15. Species encounters of all species in June 1969 enclosure. Intraspecific encounters are underlined.

			Dominance Winner and Courting Males of *Sceloporus*					
		n***	aca (5)	hor (6)	spi (4)	mag (3)	cla (1)	mel (1)
Losing Males	*acanthinus*	5	5**	1			6	5
	horridus	6		7	15		1	
	spinosus	4	1	3	7	4	7	
	magister	3	2	4		22*		
	clarki	1					0	
	melanorhinus	1						0
Females	*acanthinus*	7	31**	1	2	10		
	horridus	10	1	30*		16	5	
	spinosus	7		9	1	10	9	
	magister	1				30**		
	lundelli	1		2		2	0	
	species unknown			4	1		2	

*Significant intraspecific selection at the .05 level.
** Significant intraspecific selection at the .005 level.
***Number of individuals of each sex present in enclosure.

Also present was extremely large byb male spinosus (s-v length, 105 mm) which wb male (s-v length, 89 mm) appeared to dominate. The byb male displayed 22 times, but never fought or displayed to wb male or to any other male. Male wb challenge-postured, faced off, chased and tail-slapped byb male, but the latter only fled under extreme pressure. Often it appeared that byb male just ignored the displayer. In addition to his general lack of activity, byb male did not dominate or court other lizards. By all parameters of dominance--except that the dominant is usually the largest lizard--wb male was dominant.

While wb male was the dominant spinosus, he lost an encounter to ro male, the dominant horridus. They were both active and seemed equal. However, when ro male was removed and subordinant ryr male assumed dominance of the male horridus, he fought and defeated wb male. Male wb was inactive for the remainder of the period and no other spinosus assumed dominance. This interaction was one of a series of interspecific interactions which indicated that ryr male was subordinated by ro male with the active support of wb male. Upon removal of ro male, ryr male reversed dominance status with wb male and completely suppressed him and thus ryr male acted as the despot of both species.

All social interactions for this enclosure are summarized in Table 15. Between these two striped forms, males of horridus showed a slight preference for intraspecific dominance encounters and significant preference for intraspecific courtships. Males of spinosus did not show a preference for either intraspecific courtship or dominance. The large number of interspecific encounters of *spinosus* with *horridus* resulted from 13 encounters in which dominant *wb* male "picked on" *ryr* male while he was a subordinant of *ro* male. A possible explanation of the lack of courtship and social behavior of *spinosus* was malnutrition. Because of their secretive habits, they might not have secured an adequate diet during the winter to attain full reproductive activity to induce courtship and agonistic behavior.

Sceloporus acanthinus

In the June 1969 enclosure, *oo* male *acanthinus* quickly established dominance. He performed 202 displays (courtship and push-up) in slightly more than 2/3 of the total observation time. Before his removal, other males of his species performed 41 displays; afterwards, 63 displays. In addition, 13 of the 41 displays were performed on the first day while *oo* male was establishing his dominance. A strong dominant did not arise after the removal of *oo* male. Both *yb* and *ww* males increased their activity, but neither interacted with each other. Male *ww* performed 6 of his 11 courtships during this period and was more active displaying than *yb* male (40/17). No behavioral differences were noted between *a. acanthinus* and *a. lunaei*. Thus, it appears that they are subspecies as Stuart (1963) hypothesized. *Sceloporus acanthinus* readily recognized its species as indicated by 30 of 31 courtships initiated and five of eight dominance encounters being intraspecific (Table 15).

Sceloporus lundelli

One female, *bly*, was observed in the June 1969 enclosure. She was involved in few interactions. She was courted twice each by males of *horridus* and *magister*. No male of the uniform back line courted her. Her lack of interaction cannot be interpreted as indicative of relationships as females are recipients of interactions and do not initiate them. Other species represented by single males (Table 15) did not appear to behave in a manner that would give valid behavioral information as to their relationships to other species.

Sceloporus edwardtaylori

Both sexes of *edwardtaylori* were observed in the photographic chamber and several hatchlings were observed in a terrarium. Only females were observed in the August 1968 enclosure as the males failed to survive the summer. The females were courted by males of *melanorhinus*. Otherwise, the observed behavior was limited to movement and basking. This species showed a decided preference for tree-like forms in the enclosure.

Previously, males in the environmental chamber had not formed a hierarchy. They spent most of their time resting on the large branches where they occasionally displayed. No challenge displays were recorded.

The hatchlings were quite active, they performed challenge displays to each other in a terrarium. The hatchlings exhibited active social behavioral characteristics of the ground dwelling forms of the *spinosus* group. The adults exhibited the limited social behavior typical of other arboreal species of the spinosus group. This may indicate a basic ontological behavioral change in the social systems of different age groups of arboreal lizards.

Female Dominance

In most studies of enclosed lizards, female aggression was limited to isolated challenge displays. Dominance hierarchies were not established; only once, in females of the iguanid genus Uta, has a social hierarchy formed in an enclosure (Carpenter, 1967a). The failure of most iguanid females to form a social hierarchy poses some interesting problems in that iguanid females have been shown to be territorial (Tinkle, 1967) Hunsaker and Burrage (1969) postulated that a continuum exists between territoriality and social hierarchy and that both are related to individual distance tolerance of a particular species. Since territorial males typically form hierarchies and females do not, the view of Hunsaker and Burrage (1969) does not take into account this sexual difference. Because females of spinosus and horridus formed social hierarchies in the August 1968 and June 1969 enclosures, their interactions are detailed for possible classification of this sexual difference.

During the August 1968 study, 71 instances of aggression between females were recorded in addition to ten male-female interactions of the species spinosus and horridus (Table 16). The agressive behavior of the females was similar to that of the males, but instead of suppressing other females, they selected a rock-centered area which they defended from other females. Thus it was primarily a defense of enclosure territory as each female's activity was restricted to an area of the enclosure which she defended (Fig. 15).

Table 16. Female aggressive encounters and displays of *S. spinosus*, August 1968 enclosure. Females are listed in order of dominance.

		Winning *spinosus* female								
		wy	wg	wwg	ww	yww	wr	wo	ywb	?
Losing Female	wy	-								
	wg	1	-							
	wwg	4		-						1
	ww	2			-					
	yww	4			1	-				
	wr	2				2	-			
	wo			1			1	-		1
	ywb								-	
	w?	2	1	1		3	1	2		
Subtotal		15	1	2	1	5	2	2	0	2
horridus		4	8	0	2	0	0	2	1	5
other females		0				1				
Males			4				1		1	
Total encounters		19	13	2	3	6	3	4	2	7
Total Displays		25	1	0	4	3	1	1	1	0

The defense of their territories was not mutually

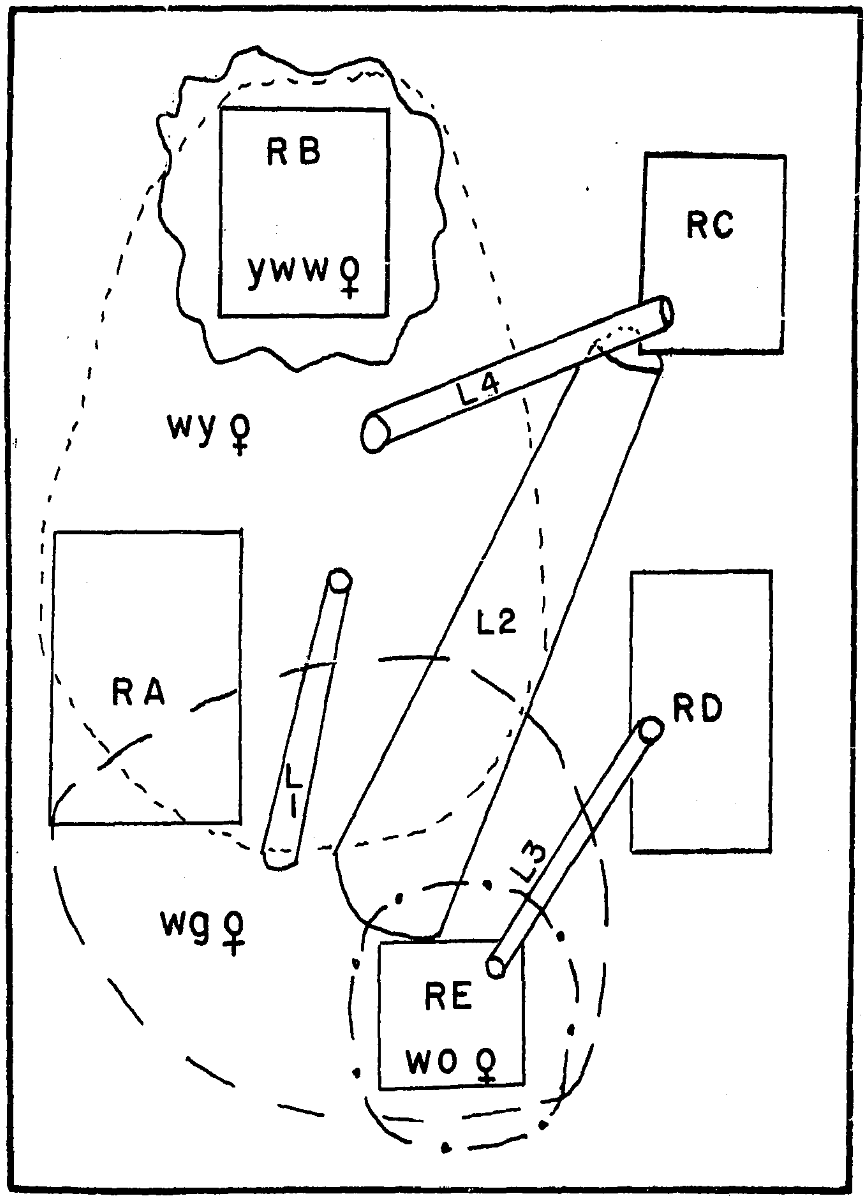

Fig. 15. Sketch of August 1968 enclosure. Activity centers of females of <u>Sceloporus spinosus</u> indicated (dotted lines). Concrete block piles (R) and logs (L) also marked.

exclusive and seemed somewhat erratic. One time a female would vigorously chase others from her area and other times she would share it. However, once committed to defending an area, they were more vicious than males. All the elements observed in male challenge displays were exhibited by females: lateral compression, dewlap extension, and facing-off. The females tail-slapped, body blocked and bit each other. However, instead of long involved sessions of displays, one would attack or chase another female in her area without warning. It appeared that female aggressive actions were not as ritualized as those of males; that they were more ready to fight than to display.

The most active female was wy spinosus; she won 19 unisex dominance interactions, 15 intraspecific, four with horridus. She confined her defense to the NW 1/3 of the enclosure containing two concrete block piles and a log pile. Besides the dominance encounters, wy female performed 25 assertion and or challenge displays. Sceloporus horridus bw female performed 10 displays, otherwise all other females performed less than four assertion displays. (Table 16)

The second most active female was wg spinosus. She was involved in 13 interactions; four with males, eight with horridus females and one intraspecific interaction. Her center of activity was associated with the SW 1/3 of the enclosure, including RA, RE and the L1 and L2 complexes (Fig. 15).

Only two other females were involved in more than three agressive interactions, yww (6) and wo (4). Female yww was associated with area RB, while female wo was found on area RE. In all these activity sites, the female defended them from females of lower rank. However, only wy female defended her area vigorously.

Females of horridus were involved in more intraspecific female interactions than interspecific (7/3). Likewise, females of spinosus interacted more often intraspecifically (30/23). Thus, although similar morphologically, the females apparently recognized their own species.

Two females were observed laying eggs: pdbg female horridus and wo female spinosus. Neither female performed displays during the digging of her nest as had been observed in females of magister (Bussjaeger, 1967). Being gravid did not cause an increase in the number of displays performed. However, pdbg female maintained a defense of the nest and nest site. Twice she rushed br male horridus while she was covering the nest. She also chased bw female and an unknown female from the nest. Her nesting site was selected and dug in a flat area north of RD, away from the highly territorial females of spinosus (Fig. 16). The spinosus female yww also dug her nest outside of the defended area in a flat spot west of RB.

Females of lunaei, horridus and especially spinosus were very agonistic in the June 1969 period. As in the previous fall, they defended enclosure sites against other females. Ninety-four successful area defenses and 12 fights in which a winner was not determined were observed. Not all females were equally active in defending an area. Area defenses are presented in Table 17.

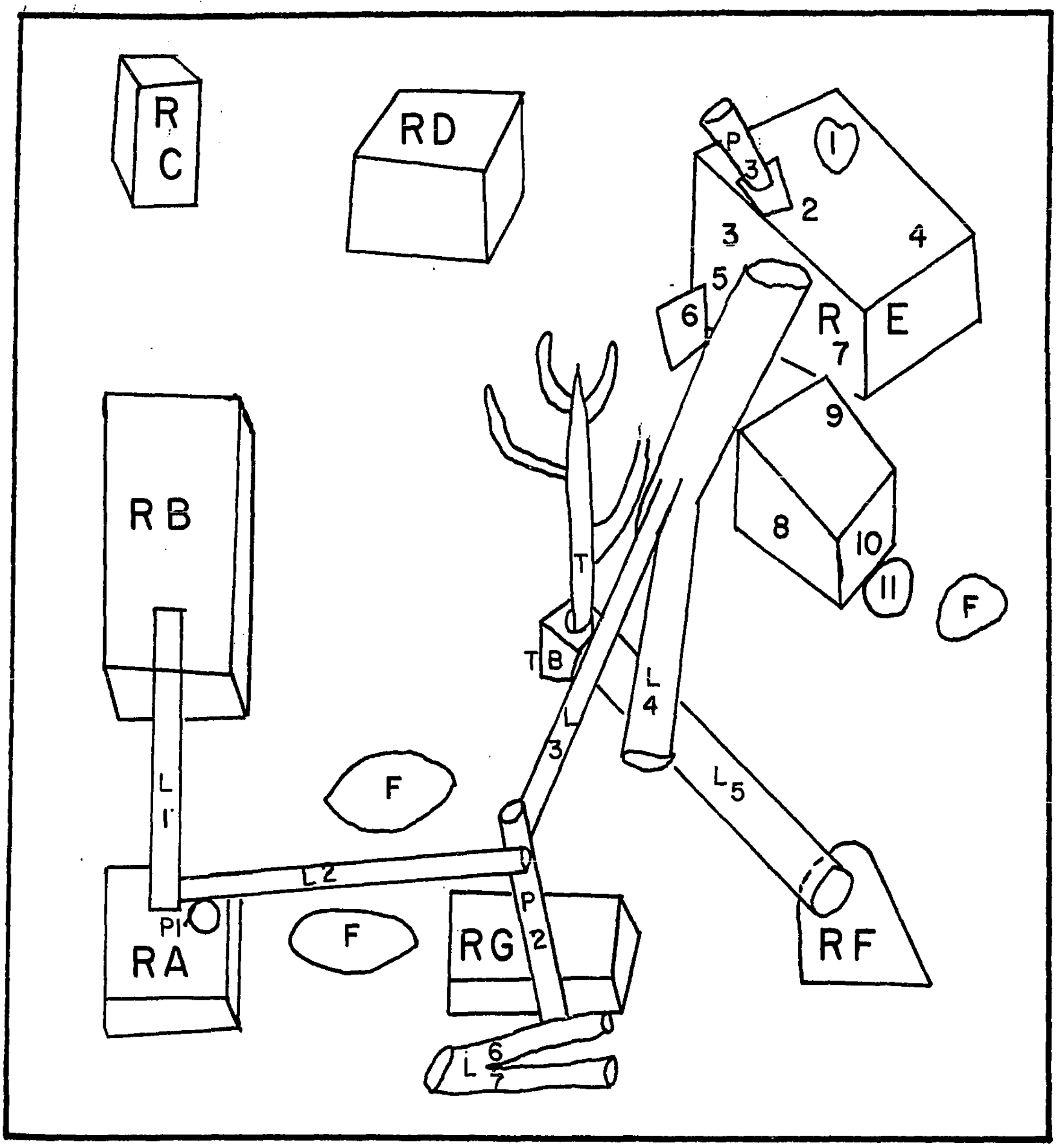

Fig. 16. Sketch of June 1969 enclosure. Concrete blocks (R), logs (L), food (F), posts (P), tree (T) and tree base (TB) are indicated.

Table 17. Total number of successful defenses of enclosure sites for females of S. *spinosus*, S. *horridus*, and S. *acanthinus*, June 1969 enclosure. Order of dominance indicated by ranking females of each species left to right. Sites are illustrated in Figure 16.

	Winning female										
	spinosus						*horridus*			*acanthinus*	
Site	wy	wg	wrg	wwg	wr	ywb	pdbg	bb	br	oo	ob
RA	6	1	10	5	1						1
RB			2	2		1				1	1
RD	1										
RE	10	16			3	1	1	4	2		
RF	1	2					1			2	
RG	8	1			1		1				
L1	3		1	2							
L2		1		1	1						
L3		1									
L5	1	1	1		2						
TB	2						3				
food		1					1				3
sand							1				
?	3					1			1	1	
No. of sites defended	9	8	4	4	5	3	6	2	3	2	2
Total encounter	35	24	14	10	8	3	8	5	4	3	6
Displays	135	15	14	34	19	6	43	6	15	106	80

Sceloporus spinosus

In the June 1969 period, five of seven female *spinosus* defended areas within the enclosure; two, *wg* and *wy*, were very active in defending areas. One, *wy* female, was the highest ranking female in that she had access to all areas of the pen; she was also the

August dominant. Other females (wwg, bb, ywb) fought with her, but none were observed to defend their area successfully against her. Initially, she defended rockpile RG from other females, chasing seven other females (all but one, spinosus) from the rock pile. Later she switched to RE8 and RE9 for her defended territory (Fig. 16).

Female wy defended rock pile RE ten times, six of these against wg female who also claimed RE. Female wg won 16 encounters over seven females there. These two females shared RE in that when wy female was out of sight, wg female defended RE from other females. Female wg never dominated wy female. In other areas of the enclosure, female wg won only six (losing 16) encounters. Female wy won all 35 encounters in which she was involved (Table 17, Fig. 16).

Except for wy female, most females tended to defend one area of the enclosure, though the area may have included several sites (Fig. 16). Female wy won encounters at the most (9) sites. Only wg female won nearly as many (8); 3/4 of them were at site RE. The next most active female pdbg, horridus, defended six areas. Other females defended fewer sites and concentrated their defense in one area. By comparing Table 17 with Figure 16, the small territorial areas can be depicted. Female wrg primarily defended RA and adjacent logs while female wwg defended RB, but overlapped into the territory of female wrg, RA and logs. They were involved in several fights of five to ten minutes duration.

Female wg defended the southeast corner of the enclosure, consisting of L3, L5, RF, RG and RE. Rock pile RE consisted of a broad, low expanse of cinder blocks; many females gathered on rocks E8 and E11 which seemed favorable for basking and were close to the feeding area. Female wr defended the northeast part of the RE complex--consisting of E5 and L2 (4/6 encounters). Rock RE5 was on the far side of L4 and was out of the view of lizards on E11. Female ywb was not observed to defend an area and was involved in only one dominance encounter.

Sceloporus horridus

Three of 10 females won interactions which indicated defense of a territory. Only one pdbg female, seemed to defend an area with vigor. She chased other females out of the vicinity of the sand area between RG and TB.

Sceloporus acanthinus

During the June 1966 period, two female a. lunaei were involved in interactions at RB and the associated food release site (Fig. 16). Female ob chased females of her subspecies (oo, oy) and a acanthinus (yy, yw). Although the only interaction observed between oo and ob females was won by ob female, oo female was considered the dominant female because this dominance encounter was not a definite clash, but one of avoidance. Also, female ob performed 3/5 of her displays, one half of her defenses of areas RA and RB during the last part of the observation period (2/9 of total time) when oo female was dying. Female oo did defend and was active on area RB and RF prior to her death. Most (5/7) of the a. lunaei and a. acanthinus females did not participate in defense of an area.

Interspecific Female Encounters

Species interactions are depicted in Table 18. Females of *horridus* interacted only with their own species, indicating their discriminatory ability. Likewise, females of *acanthinus* reacted predominantly with their own species. However, females of *spinosus* reacted only slightly more often intraspecifically than interspecifically. This seemed to indicate a lack of ability to distinguish their species.

Table 18. Aggressive encounters between females of *S. spinosus*, *S. horridus* and *S. acanthinus*, June 1969 enclosure.

			Winning Female	
	n*	*spinosus* (7)	*horridus* (10)	*acanthinus* (7)
Losing female:				
spinosus	7	39		1
horridus	10	29	16	
acanthinus	7			4
unknown sp.		5		1

n* - number of females present.

One index of dominance was the total number of displays performed which related to their total activity. In all three species, the most agonistic female performed the greatest number of displays; however, the next highest ranked female did not necessarily perform the second largest number of displays (Table 17).

Sceloporus magister, *blo* female, performed 138 displays even though she was the only female of her species present. One reason she performed so many displays, in my opinion, was that dominant male *blo magister* courted her often.

CHAPTER VI

DISCUSSION

One difficulty in deriving phylogenetic trees results from the different evolutionary rates of the characters studied. Different characters--morphological, karyotypical and behavioral--are subjected to different selective pressures and thus evolve at different rates. Data are being collected to determine the rate at which characters can evolve. For example, morphology has traditionally been considered a conservative trait. Estimates for the formation of subspecific variations in vertebrates had been for at least 10,000 years (Mayr, 1963). Johnston and Selander (1964, 1967) have found variations in introduced populations of House Sparrows, *Passer domesticus*, corresponding to the subspecies level, which have evolved in less than 50 years. Therefore, each character and type of data must be subjected to different interpretations to arrive at a scheme that reflects genetic affinities. Which factor is weighted, which character is primitive and what criteria are used to make these decisions has prompted a vigorous discussion among systematists. This is the focal point of the arguments by proponents of both the classical and phenetic methods of taxonomy. Both agree, however, in the multi-phasic approach to studying phylogenies. One must use all possible characters to synthesize the most realistic scheme.

The initial purpose of this study was to ascertain the usefulness of behavior in determining the phylogenetic relationships of the _spinosus_ group of _Sceloporus_. In any comparative behavioral study, one must initially assume the current systematics are correct. If the behavioral data clash with the current scheme, one must use other independent sources of evidence to avoid circular reasoning (Hinde and Tinbergen, 1958). Since Smith (1939) published his phylogeny of the genus _Sceloporus_, additional data has been gained from studies in zoogeography and herpetogeny of Mexico and Central America, from karyotypic data and the other interpretation of iguanid and _Sceloporus_ behavioral data. Before assessing the present behavioral data, a review of other pertinent evidence is in order.

Evolutionary Evidence of Karyotypes

Karyotypic evolution tends to be conservative when compared to other characters; thus it can serve as a "bench mark" to document suspected relationships between species (Gorman, Atkins and Holzinger, 1967). However, Harlan (1969) emphasizes that chromosomal traits are no more significant than phenotypic traits and are useful only when they complement phenotypic data.

The main mechanism hypothesized for karyotypic evolution among lizards is chromosomal fusion; thus, the general trend is that derived species have lower chromosome numbers than primitive species (Gorman, Atkins and Holzinger, 1967). The alternate hypothesis of centric fission--resulting in an increase of chromosome number--is not widely accepted, but is apparently feasible (John and Hewitt, 1968; and Hall, pers. comm.). Karyotypic evolution occurs when the mutant karyotype is present in high enough frequencies in an isolated population so that a homozygotic mutant karyotype may arise and be selected. A major factor inhibiting karyotypic change is that heterozygotes between normal and mutant karyotypes are semi-sterile. Since heterozygotes produce few offspring, as long as the mutant population (once established) outnumbers the normal karyotype, selection can act on the two populations until reproductive isolation is achieved. However, mutant populations can easily be swamped by the parent population if the latter invades their habitat.

Similarity of gross karyotypes does not indicate genetic closeness per se. Similar karyotypes may represent convergence toward a mechanically satisfactory structural change (White's Principle of Homologous Change, Gorman, Atkins and Holzinger, 1967). Genetic content, arrangement and especially changes within the chromosome by the processes of inversion, duplication, deletion and centromere relocation, are not detected in normal karyotypic studies. One would need to study cells in the pachytene stage of meiosis to detect these differences.

Karyotypes of the spinosus group of Sceloporus are being studied by two researchers--Charles C Cole at the University of Arizona and William Hall III at Harvard. At this time, karyotypes have been determined for most species of the spinosus group of

Sceloporus, except lundelli (Table 19). Based on these data, two hypotheses are proposed which differ in basic premises. One hypothesis, used by the Arizona group, is that the primary method of karyotype speciation is centric fusion and that the common karyotype number of iguanids (2n = 36) is not primitive, but represents a derived state. Lowe, Cole and Patton (1967) supported their contention that clarki (2n = 40) is primitive to magister (2n = 26), with ecological and biogeographical data. On the bases of the principles used, they support the present phylogeny of Smith (1939). The derived forms of the spinosus group of Sceloporus have the lowest karyotype according to this phylogeny (Fig. 17A).

Hall's basic contention (pers. comm.) is twofold: 1) centric fusion of fission can occur; 2) the common karyotype (2n = 36, 12M + 24m) found in most iguanid genera is primitive (Gorman, Atkins and Holzinger, 1967). Analyzing the data on these premises drastically modifies Smith's (1939) phylogeny for the spinosus group of Sceloporus (Fig. 17B). In this case, because of its primitive karyotype, orcutti must be considered near the main line of evolution. After orcutti split off, there are two possible ways to derive magister and clarki. Centric fission could occur resulting in a pre-clarki form (2n = 40) which then underwent centric fusion to magister (2n = 26) and clarki (2n = 40). The other possibility is that a common ancestor (2n = 36) concurrently underwent fission to form clarki (2n = 40) and fusion to form magister (2n = 26). The first hypothesis would agree with Lowe et al.

Table 19. Karyotypes of the spinosus group of Sceloporus and some related species.

Species		2n*	Chromosome Arrangement (M = Macrochromosome) (m - microchromosome)
clarki		40**	20M + 20m
melanorhinus		40	20M + 20m
orcutti		36	12M + 24m
magister		26**	12M + 14m
edwardtaylori		22	12M + 10m
spinosus		22	12M + 10m
horridus		22	12M + 10m
olivaceus		22	12M + 10m
cautus		22	12M + 10m
undulatus		22**	12M + 10m
formosus		22	12M + 10m
asper	male	31	12M + 19m
	female	32	12M + 20m
jarrovi	male	31	12M + 19m
	female	32	12M + 20m

*Hall (pers. comm.) has generously supplied or substantiated all karyotypes.

**Lowe, Wright and Cole, 1966.

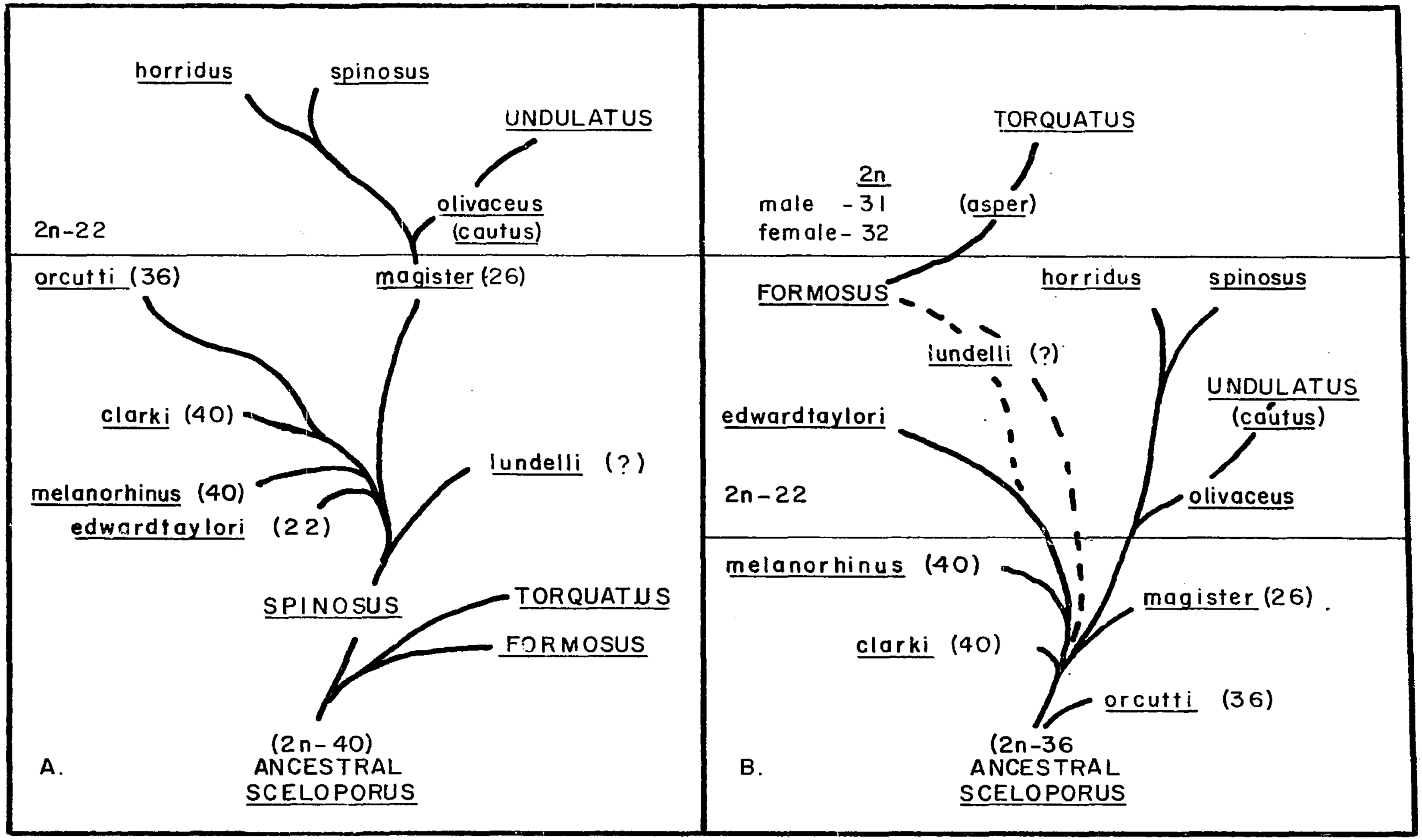

Fig. 17. Hypothetical phylogenetical schemes of the species of the spinosus group of Sceloporus based upon my interpretation of two karyotypic theories of evolution and dorsal color patterns. A Centric fusion method, primitive karyotype 2n = 40. B. Centric fusion and fission method, primitive karyotype 2n = 36.

(1967) as they postulated the fusion of micro- and macrochromosomes to derive *magister* from *clarki*. The configuration of the "broken" chromosomes of *clarki* matches the fused chromosomes of *magister*, and the total amount of genetic material appears the same. If *clarki* and *magister* were derived from a common ancestor, their chromosomes could probably match with about the same reliability shown by (Lowe et al. 1967). The karyotypes of *clarki* and *magister* need to be compared to *orcutti* to discern the possible relationships of these three species. Once *magister* and *clarki* are derived, speciation proceeds the same in the *magister* line of both phylogenies (Fig. 17).

The formation of the uniform back line is not easily derived as the placement of *melanorhinus* and *edwardtaylori* is difficult. Undoubtedly, *melanorhinus* is close to *clarki*; but *edwardtaylori* could be derived from a pre-*clarki*-*melanorhinus* form, or possibly *clarki* itself gave rise to *melanorhinus* which then radiated to form *edwardtaylori*. This question of derivation probably will not be cleared up until the karyotype of *lundelli* is examined. This is especially true in ascertaining the relationship of these species of the uniform back line to the *formosus* group.

Herpetogeny

Smith (1939) published his phylogenetic ideas on the species of *Sceloporus* without elaboration of his reasoning. On the basis of the data presented, he primarily used morphology (size, scalation and coloration), ecology and distributional patterns, probably interpreted on the basis of E. R. Dunn's (1931) ideas of herpetogeny (development of the herpetofauna) of the region and Schuchert's (1935) scheme of physiographic events. However, neither work was then cited by Smith (1939). Later, Smith (1949) described the biotic provinces of Mexico and elucidated some of his basic assumptions on reptile phylogenies. "Natural phylogenetic trees thus almost invariably have their bases in the plateau area, and the branches directed from that area" (Smith, 1949). Furthermore, Smith (1949) stated "Known herpesian phylogenies establish securely the fact that the Mexican and Guatemalan plateaux are populated by primitive species." However, this basic assumption does not seem to apply either to the origin of the genus Sceloporus or to the speciation of the spinosus group of Sceloporus. Smith emphasized the important effect of the plateau and mountains as centers of origin, refuge, isolation and dispersal. These effects are still important, but recent reviews and papers have emphasized the development of the herpetofauna of Mexico--especially Sceloporus--with the development of the Madro-Tertiary Geoflora, after which the plateaus of Mexico were formed and influenced the speciation of the genus.

The impetus for the changing viewpoint on the herpetogeny of Central America was the development and documentation of the evolution of the Madro-Tertiary Geoflora of Northwest Mexico by Axelrod (1958) and others. Using his scheme, Savage (1960, 1963, 1966) and Tihen (1964) developed herpetogenic theories of the southwestern United States, Mexico and Central America. In addition, papers dealing with the phylogenies of related genera (*Uma*, Norris, 1958; *Uta*, Ferguson, 1969; and *Phrynosoma*, Presch, 1969) have utilized these schemes which support the following hypothesis which I have synthesized for the *spinosus* group of *Sceloporus*.

Briefly, the plant species composing the Madro-Tertiary Geoflora developed in late Mesozoic or early Cenozoic in response to increasing aridity. The area in which they developed was a moist tropical lowland in what is now southwestern United States and northwestern Mexico. Within the lowland areas, xeric edaphic pockets formed which were the major sites for the development of the characteristic species of this geoflora. Most forms similar to the modern species had evolved by the Oligocene. During the Miocene and Pliocene, the aridity became more severe and the temperature became cooler, allowing the developing geoglora to spread over southwestern North America. Concomitantly, extensive orogeny and vulcanism occurred in the Pliocene which formed the present day physiographic features and initiated the development of the characteristic plant formation of the Madro-Tertiary Geoflora: desert, grassland, arid subtropical scrub, chaparral and pine-oak woodland.

The basic points of the geoflora development are correlated with the major step of herptile evolution. Savage (1960) placed *Sceloporus* as a member of the Young Northern Element. This group was derived originally from tropical American ancestors in xeric extra-tropical portions of Mexico and southwestern United States. The group includes the sceloporine group of iguanids as well as other reptiles. *Sceloporus* was the only sceloporine genus to radiate through Central America, but Savage (1966) lists six non-sceloporine genera which have the same distribution pattern.

According to Savage (1960, 1963), the sceloporine ancestor developed with the forming elements of the Madro-Tertiary Geoflora. By the Pliocene, with the geoflora spreading due to increasing aridity, the modern lizard genera evolved and spread over Mexico. Also, during the Miocene and Pliocene, extensive orogeny and vulcanism resulted in the geographic features that led to the forming of the main plant associations of the Madro-Tertiary Geoflora. This appeared to initiate the differentiation of the species and species complexes of Sceloporus (Savage, 1960). Most of the species groups of Sceloporus reflect their origin by an association with a particular vegetative formation. Following this basic division, speciation occurred primarily in the Pleistocene epoch in response to the glacial cycles.

Further evidence for a Madro-Tertiary evolution of Sceloporus is derived from associated genera. Uma, Uta and Phrynosome are grouped with Sceloporus in the sceloporine group of iguanids (Presch, 1969). The evolution of these three genera has been traced with the development of the Madro-Tertiary Geoflora (Norris, 1958; Ferguson, 1969 and Presch, 1969). It seems likely that Sceloporus has a similar origin. The temporal period proposed for the other genera corresponds to that proposed for Sceloporus. However, these other genera have specialized for restricted niches and this probably hindered their speciation and limited their distribution. Because the genus Sceloporus is of a plastic generalized nature, it has responded to the selective pressures of the diverse habitats by radiating into a large number of species and species complexes.

Schemes of speciation within the spinosus group of Sceloporus are limited only the imagination of the speculator and the rate of evolutionary change ascribed to the group. Most schemes of the evolution of the spinosus group initially entail isolation of the two lines--uniform back (clarki line) and dorso-lateral striped back (magister line)-by the eruption of the Sierra Madre Occidental and the trans-volcanic belt during the Miocene (Fig. 18A). This would divide the ancestral form so that one line evolved with the arid tropical scrub vegetation of the west coast (uniform back line) while the other line encountered the developing desert formation of the up-lifting plateau. One basic difference of the two major schemes proposed for Sceloporus is that Smith (1939) would place this origin in southern Mexico (Oaxaca) while Savage (1966) would place it in northwestern Mexico or Arizona (Fig. 18A). From his scheme, Smith (1939) would derive lundelli by isolation of the ancestral form in Yucatan. Sceloporus lundelli would then represent the connecting form to the formosus group from which the spinosus group arose. Savage (1966) would probably place lundelli as the most distinct and distant form and as the connecting species which gave rise to the formosus group (Fig. 18B).

After this basic division into the striped and uniform back forms, Smith (1939) and Savage (1966) would accomplish speciation in much the same manner except Smith (1939) would emphasize a

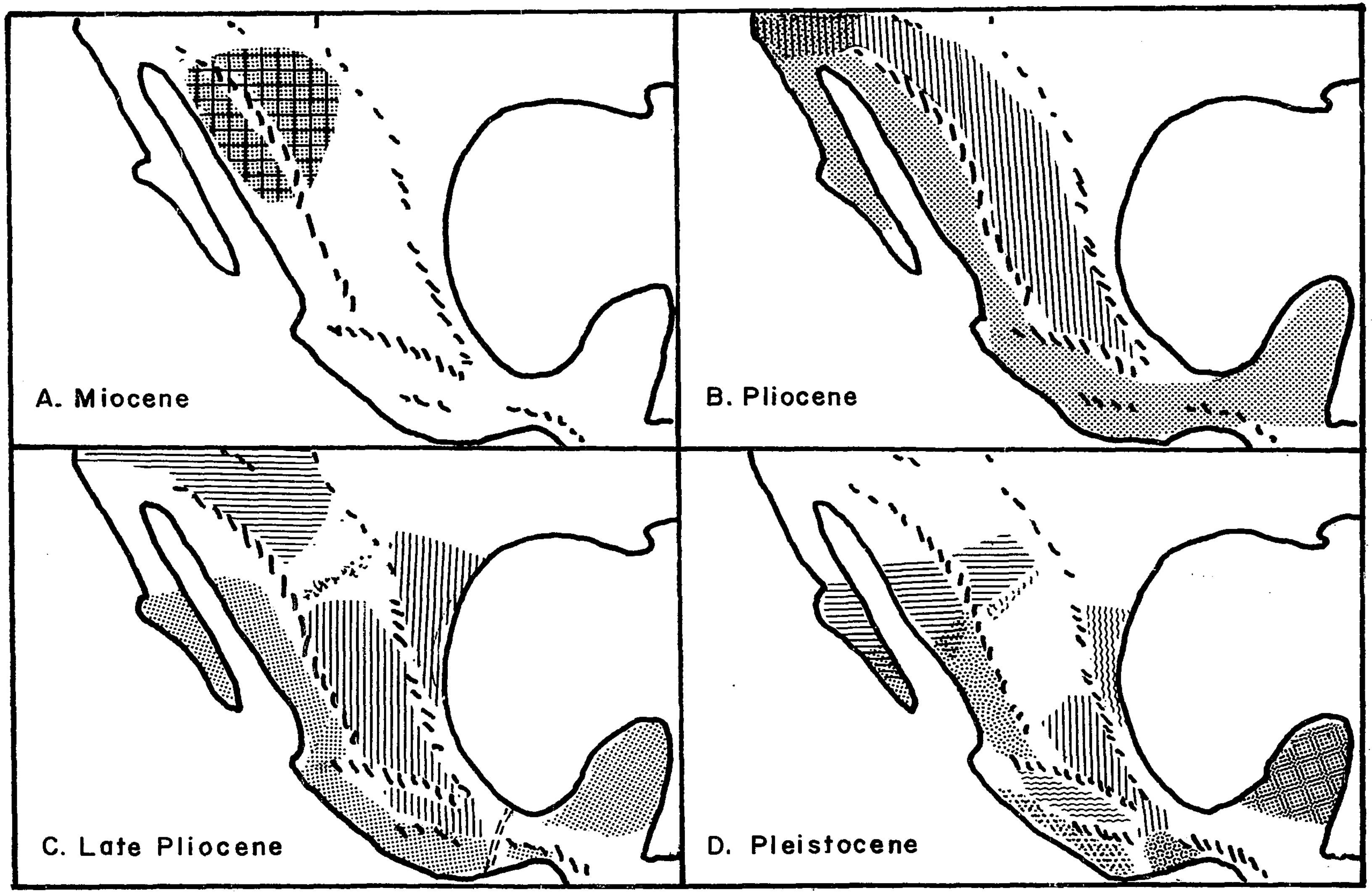

Fig. 18. Hypothetical origin of *spinosus* group of *Sceloporus*. Uniform back lizards indicated by dots; striped back species indicated by lines. Species of "D" can be determined from Figures 3 and 4. See text for explanation.

northward trend in speciation while Savage (1966) would emphasize a southward trend. The zoogeography of the spinosus group of Sceloporus according to Savage (1966) will be examined in detail.

Once the two basic forms evolved, they radiated with their flora to cover the central Mexican plateau (striped back line) and the western coast (uniform back line). With the cooling and increasing aridity of the Pliocene, a southern shift in the populations of the basic forms occurred. Probably a pre-orcutti was isolated in the Baja peninsula from a uniform line ancestor by this southern shift. This seems more likely than Savage's (1960) hypothesis of its derivation by restriction to the cape during a period of Pleistocene glaciation. Smith (1939) states, "S. orcutti is rather definitely the western derivative of clarkii." Also, the high chromosome number of orcutti would indicate an early derivation from the uniform line and its purple dorsal coloration, found also in magister, would indicate an affinity for the striped back line (Fig. 18B)

Also in accordance with Savage's (1966) and Smith's (1939) hypotheses, the striped line split early into two lines, pre-magister which was isolated and developed exclusively with the North American deserts and a pre-spinosus line of the central plateau (Fig. 18C). Because of the similarities of clarki and magister (Lowe et al., 1967) and the differences in chromosome numbers in the pre-spinosus line and magister, the division of magister should have occurred early in the evolution of the spinosus group so that affinities to both groups are maintained. Chromosomal data support the joint evolution of spinosus, horridus and olivaceus while morphological and behavioral data support the close association of the former pair.

Thus, pre-spinosus gave rise to olivaceus fairly early--isolated by the Sierra Madre Oriental in the Pliocene--and to horridus and spinosus in early Pleistocene. Apparently, horridus "slipped" through a gap in the trans-volcanic belt and speciated in the xeric communities on the western slope between the coastal uniform back species and the inhospitable higher montane habitats. The derivation of horridus must have occurred south of Mexico City as the subspecies h. horridus is closest to spinosus.

The derivation of the uniform back line is unclear. Apparently, it spread rapidly southward with the expanding arid coastal vegetation during the Pliocene (Savage, 1966; Fig. 18B). The terminal populations of this movement speciated into lundelli (Yucatan) and edwardtaylori (Tehuantepec). These latter species developed while separated from the rest of the Mexican population by a xeric lowland isthmus barrier (Fig. 18C). Sceloporus edwardtaylori has a derived chromosome number which could explain its rapid evolution without a strongly effective dispersal barrier. The remaining uniform back line split into two species (orcutti already derived); northern clarki and southern melanorhinus (Fig. 18D). The latter shows an affinity for lundelli since both have orange ventral coloration in males.

Subspeciation within the spinosus group was accomplished since the Pleistocene period of glaciation. The method of subspeciation in *magister* was probably similar to that detailed for *Uta* by Ferguson (1969) since their distributions are sympatric. During one or more of the four Pleistocene glaciers, *magister* retreated into three desert refugia: Baja California cape, Sonora and Chihuahua. After the glacier retreated, these ancestral subspecies radiated into the North American deserts to form the numerous subspecies of *magister*. The lack of subspecies in *spinosus* and *olivaceus* also probably resulted from periods of glacial maxima during the Pleistocene. During these periods, inland temperatures dropped lower than coastal temperatures which were moderated by the ocean. Thus, *spinosus* was forced into one refugia, the Oaxacan highland. After the glacial period, *spinosus* radiated from this center. This would support Smith and Smith (1951) who considered *s. spinosus* and *s. apicalis* to be derived from the Oaxacan form, *s. caeruleopunctatus*. Likewise, the lack of subspecies in *olivaceus* and its restriction to an arboreal habitat--the only striped back form so limited--could have resulted from its being confined to a small east coast wooded refugium. Thus, *olivaceus* might represent a small genetic sample of the original population. The northern species, *clarki*, radiated into a number of relict subspecies due to isolation during the Pleistocene epoch. Otherwise, subspeciation in the west coast forms seemed dependent upon normal geographic barriers as they were not affected by the drastic temperature changes as were the inland species.

Display Behavior

Comparison of species specific behavior patterns can be analyzed from two bases: similarities in the gross aspect of the display and in the elements (units) of the display. These in turn can be subjected to two basic postulations of comparative studies: 1) the similarities (and differences) reflect phylogenetic homology; 2) the characters reflect adaptations to other environmental factors and not genetic affinities.

That behavior patterns do have systematic significance is well documented by Hinde and Tinbergen (1958). The requirements stated by them for the usefulness of a behavioral character for phylogenetic studies are met by the display behavior in iguanids Ferguson (1969) fulfilled each of their postulates, point-by-point, in ascertaining the validity of the display behavior of *Uta*. These points are equally valid for the genus *Sceloporus*. Briefly, they are: 1) the displays are inheritable (innate). This is well documented by hatchling iguanids performing species specific displays (Carpenter, 1967; pers. obs. on *Sceloporus*) and recently by hybrid lizards from two species of *Anolis* performing hybrid displays (Gorman, pers. comm.). 2) the variation within the group is less than between groups at the same taxonomic level. The extent of variation depends upon the genus, species or species group, but the variation is extremely small at the population level. For example, Clarke (1965) found generic differences in the displays of allopatric forms of *Holbrookia*, *Callisaurus* and *Cophosaurus*.

Gorman (1968) found species and species-group differences in members of the roquet species group of Anolis. Ferguson (1969) found racial and species distinctiveness in Uta. Jenssen (1969) found population differences in Anolis. In the present study, depending upon the species, each was represented by one to several distinct displays. Variations were found at the racial level in spinosus, horridus and clarki; but not in the widely distributed magister. Much is still unknown about the amount of display variation in all the forms of the spinosus group of Sceloporus. However, the displays of the spinosus group are typical of those described for Iguanidae. In the first five categories of Carpenter (1962), the displays of the spinosus group differed in no significant respect from undulatus and most other known displays of Sceloporus. Some widely separated species groups of Sceloporus seem to have behavioral characters valid at the species group level. Sceloporus merriami of the merriami group typically performs displays using all four legs. In the variabilis group, the extreme lateral posturing is associated with the display. As with most species of Sceloporus, all lizards of the spinosus group used only the fore legs for the display, but in performing high intensity displays, they rocked back so as to appear to use all four legs. The display-action-patterns were the same for both challenge and assertion displays for both sexes of all species. 3) the stability of the display through geologic time has been established in Uta (Ferguson, 1969) and the lack of geographic variation in most species of the spinosus group of Sceloporus indicates that the display is stable. 4) The final criterion is understanding of the function of the display so that possible factors affecting the display can be analyzed. Hunsaker (1962) and Jenssen (1969) have shown that the display can function as a species specific communication signal in that females showed a preference for the proper species display. Thus, the validity of display behavior as a systematic tool has been well established.

The generalized patterns characteristic of each species of the _spinosus_ group of _Sceloporus_ are presented (Fig. 19). The cadence of those displays taken from Bussjaeger (1967) may be in error and not represent a faster cadence for the species of that study. The film speed of the camera then used was not calibrated. The same brand of camera used in this study was found to be 25% faster than indicated by the dial setting. A similar error in the camera used in the 1967 study would result in the apparent temporal differences seen here. However, temporal differences between the species are probably not as important as the pattern and components of the display. The cadence of the display of _Anolis carolinensis_ has been shown to vary directly with temperature (McCardel, pers. comm.). The units selected for comparative characters are summarized to facilitate comparison of the species displays (Table 20). The displays of the species are characterized by the presence or absence of these selected display components.

Common Display Patterns

In comparative studies of lizard display behavior, most emphasis had been placed on the patterns formed. This was true of Carpenter (_Tropidurus_, 1965), Clarke (sand lizards, 1965), Lynn

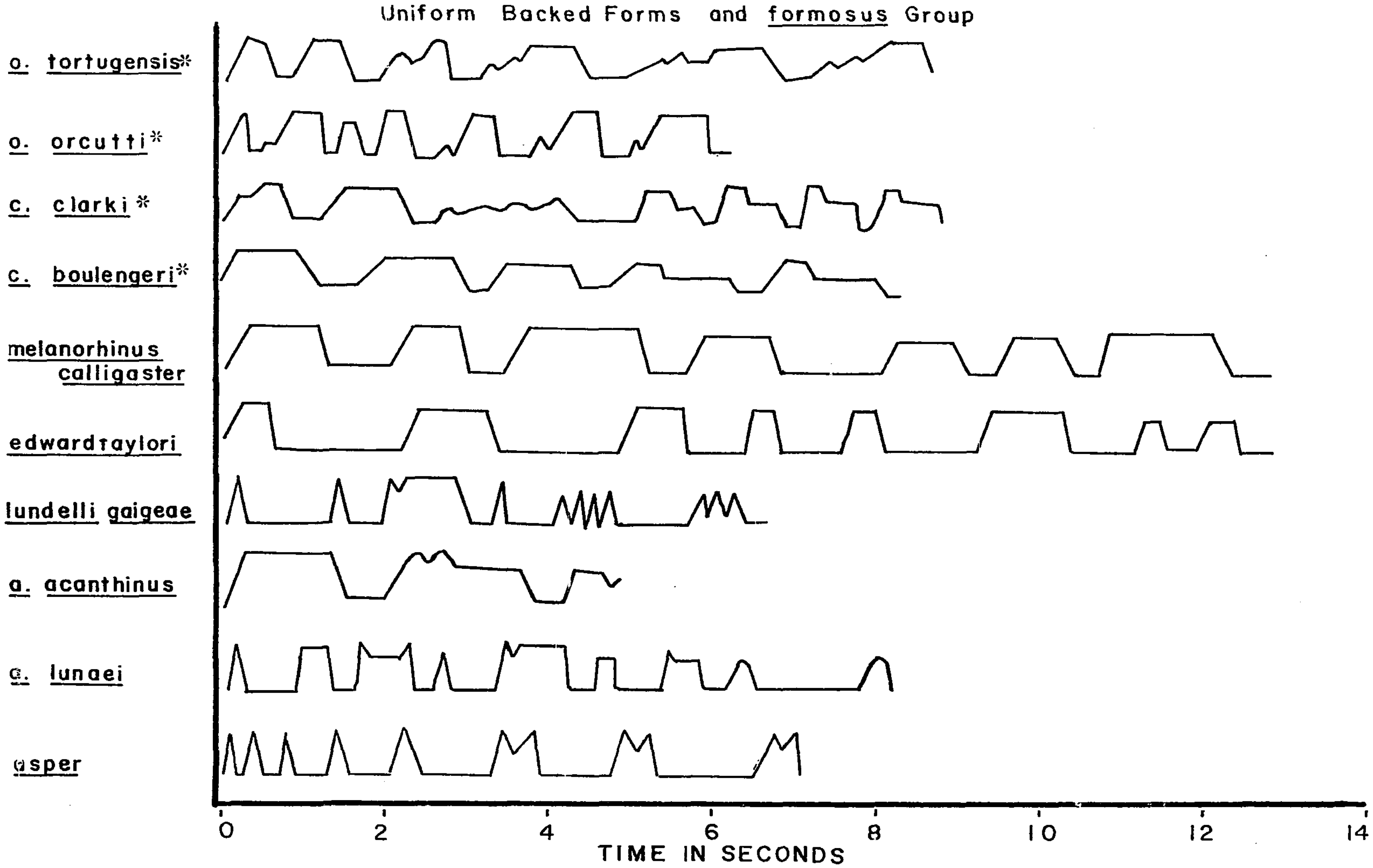

Fig. 19. Averaged display-action-pattern graphs of the *spinosus* group of *Sceloporus* and related species. Explanation in text and Table 20. *Bussjaeger (1967), cadence may be slow.

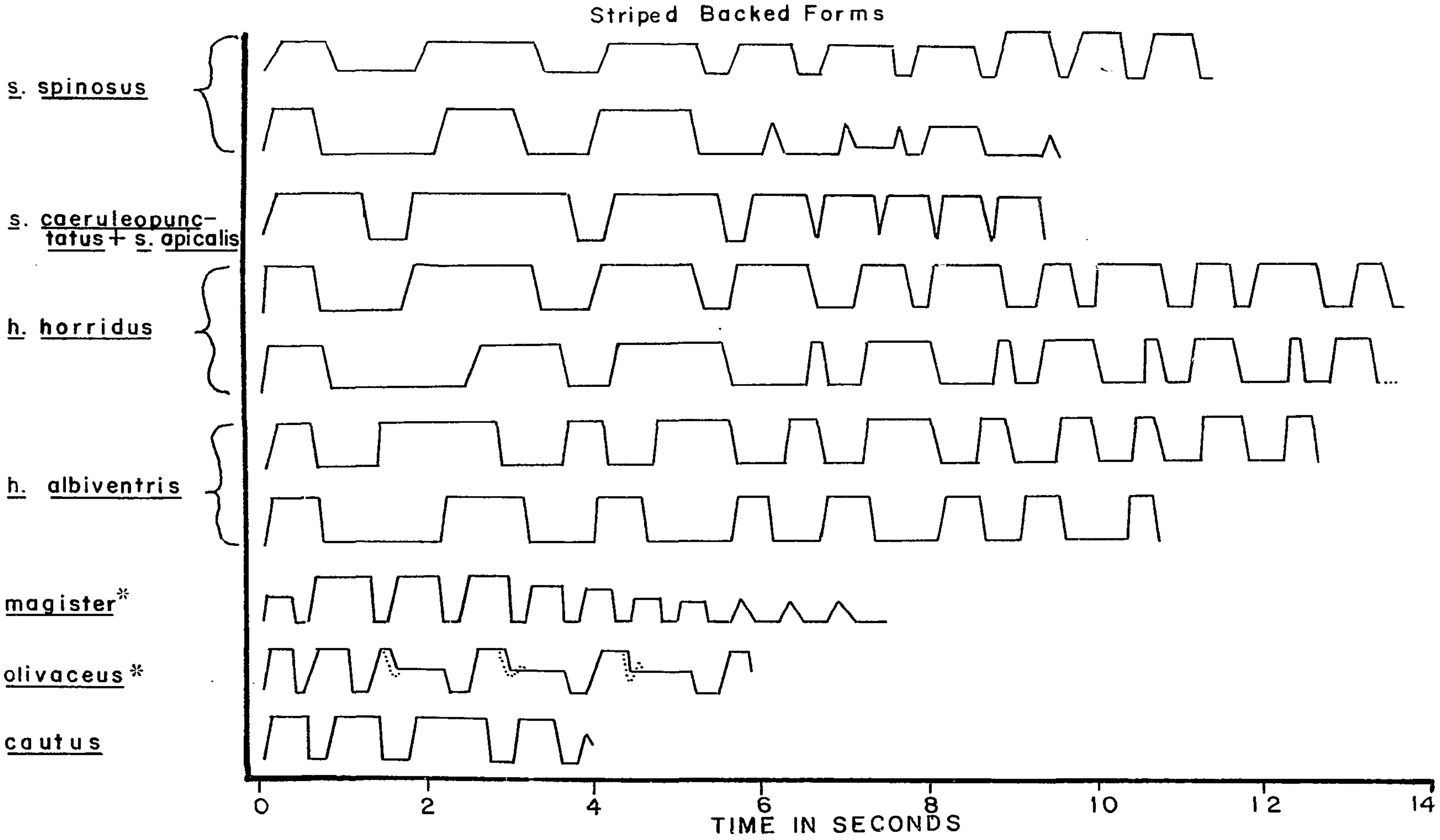

Fig. 19. Continued.

(*Phrynosoma*, 1965) and Gorman (*Anolis*, 1968). However, Thompson (1968) stressed the component elements composing the song structure in ascertaining relationships of various buntings. Thompson's method seemed useful in comparing displays of this species group, as homologous units were used to ascertain relationships.

In analyzing lizard display-action-patterns for phylogenetic significance, one should keep in mind the possible sources of variation besides evolution. Ferguson (1969) discussed four factors which could cause divergence in the display of populations of the same species. These factors are: 1) character displacement; 2) predator selection; 3) epistatic selection; and 4) genetic drift. Several other explanations are possible; the display could be modified by a change in its use or function (*Phrynosoma*, Lynn, 1965) or by adaptation of the display to the habitat. Another variation would be an adaptation to increase the visual effectiveness of the display as a communication signal. In addition, chromosomal changes within the species could alter the display by loss of part of the genome controlling the display.

The display-action-patterns of *lundelli* *gaigei* of the *spinosus* group and *asper*, *acanthinus* *acanthinus* and *a*. *lunaei* of the *formosus* group were quite similar with peaked single units and multiple units. *Sceloporus* *asper* and *lundelli* seemed to share more elements; the display of *a*. *lunaei* tended to have a much slower cadence as it was composed of more multiple units. The displays of *a*. *acanthinus* seemed distinct from those of *a*. *lunaei*, but the sample was so small, that subspecific differences were only suggested (Fig. 19).

The display-action-patterns of *magister*, *spinosus* and *horridus* were similar. The displays of all three species were composed of various single and peaked units which formed a pattern of three introductory units and a series of single units. In *horridus*, the single units formed an alternate pattern of short and long units. Further relationships were shown by the peaked units terminating some unusual *spinosus* displays as these were similar to the peaked units terminating the normal displays of *magister*. These aberrant displays of *spinosus* also suggested that two display-action-patterns were fixed in individuals and subspecies of this species. Multiple patterns have been observed in *horridus*; it is the only species of lizard known in which individuals perform two distinct display-action-patterns which are constant within a subspecies.

Two of the most distinctive display-action-patterns were those performed by *melanorhinus* and *edwardtaylori*. Their displays were similar and involved single units performed at a slow cadence with a distinct pattern of units. Both species repeated patterns composed of multiple single units, but the display of *melanorhinus* lacked introductory units. Marler and Hamilton (1966) stated that species specific behavioral data was most valid between allopatric species. Except for *melanorhinus*, most species of the *spinosus* group have primarily allopatric distributions. The distribution of *melanorhinus* is sympatric with *horridus* and *edwardtaylori* and barely overlaps *clarki* (Fig. 3, 4). Perhaps this explains why *melanorhinus* has both the most aberrant coloration and display.

Its unusual display could have resulted from character displacement (selection of different display patterns to prevent mismatings) or the pleiotropic effect of genes selected for the unusual color patterns of melanorhinus.

The only other similar sized lizard of the genus Scelop orus whose distribution overlapped any member of the spinosus group belonged to the torquatus group. This was a distinct group, highly specialized for rocks and rock-crevice habitat niches and with a distinctive outlined collar mark. Species discrimination tests between species of these groups, olivaceus and poinsetti, have shown the two species can discern one another (Pyburn, 1955) The display-action-patterns of the species of the torquatus group of Sceloporus, described by Hunsaker (1962), appeared to be quite different from the spinosus group. Carpenter (pers. comm.) has found the laboratory behavior of the species of the torquatus group to be inhibited. It appears that Hunsaker analyzed very weak assertion displays as the complete challenge display are very different.

The display-action-pattern of olivaceus contained elements of both magister and clarki. The initial single units of olivaceus were similar to those of the magister line while the terminal units resembled the multiple units found in clarki. The displays of orcutti (mainland) were similar to clarki as their display-action-patterns began with single introductory units and terminated with multiple units. These similarities reflect supposed phylogenetic relationships between the species associates.

General phylogenetic trends of display-action-patterns had been shown in three genera of iguanids. The displays of Uta (Ferguson, 1969), Phrynosoma (Lynn, 1965, reinterpreted according to Presch, 1969) and Anolis (Gorman, 1969) had shown a pattern in which the most primitive display consisted of a series of short uniform units. The derived displays consisted of longer displays with units of various lengths forming a more structured pattern. These relationships were better expressed in the continental genera than in the insular Anolis. These general trends appeared to be substantiated by the display-action-patterns of the spinosus group of Sceloporus. Both the clarki-line and magister-line showed a modification of the display from a uniform series of units to a more varied series (magister to horridus; clarki to melanorhinus).

Before further assessment of the phylogenetic significance of the displays, the alternate hypothesis, the effect of habitat on the display-action-pattern, should be discussed. Two types of display-action-patterns were apparent. The display of terrestrial forms (magister, spinosus, horridus and orcutti) seemed to consist of repeated single units which got progressively shorter. The arboreal forms (clarki, melanorhinus, edwardtaylori and olivaceus) had display-action-patterns which were more complex and had a slower cadence. This is true of other arboreal species; Urosaurus ornatus had slow complex displays (Carpenter and Grubitz, 1961). Other terrestrial or ground dwelling lizards had quick, simple displays--Uta (Carpenter, 1962b, Ferguson, 1969), Phrynosoma (Lynn, 1965), Uma (Carpenter, 1963) and Holbrookia (Clarke, 1965) The displays of Phrynosoma were very reduced, perhaps in response to both their ground dwelling habits and their lack of social interaction (Lynn, 1965).

In the *spinosus* group, the arboreal species had a very restricted habitat niche; but the terrestrial species were more ubiquitous. One exception was the primarily tree dwelling species *clarki*, Smith (1946) reported that it was often found in rocky situations. Mainly terrestrial species, *spinosus*, *horridus* and *magister* have been taken exclusively from trees or tree-like objects. With such opportunistic species, one might expect the different environmental factors that might possibly alter a display pattern to cancel each other, thus promoting retention of the basic display pattern. Therefore, a ubiquitous species would be expected to have a generalized display that would reflect phylogenetic closeness rather than habitat utilization. This seemed to be the case in the above terrestrial species whose displays were similar, with little variation within each of their displays. It seems likely that the displays reflect a combination of both habitat and phylogeny.

Habitat selection on the display could explain why the display-action-pattern of *olivaceus* is different from other striped back forms. This species may have been modified from an ancestoral terrestrial form to an arboreal form. This fits the herpetogeny scheme previously outlined; that it evolved in a forest refugium in the northeast coast of Mexico from a pre-*olivaceus* terrestrial form. Similarly, Savage's (1960) hypothesis for the speciation of *orcutti* was that it originated in a thorn forest refugium in the cape of Baja and became secondarily adapted to a boulder habitat.

This could explain the arboreal multiple units in the displays of *orcutti*, a terrestrial species.

Social Behavior

Observations of mixed populations of lizards provided the opportunity to observe interactions in situations approximating field conditions. The individuals demonstrated their behavioral preferences by their free choice of interactions within and between species. These interactions indicated significant behavioral relationships; but the presence of multiple factors compounded the difficulty of ascertaining these relationships. Both intrinsic and extrinsic factors complicated the interpretations of the behavioral results--weather, context of behavioral interactions, seasons, and so on. For example, hormone levels, acting with the season of the year can influence the behavioral interactions. Testosterone injections induced gravid coloration and behavior in female *Holbrookia* (Clarke, pers. comm.) and mating behavior in out-of-season male *Uta* (Ferguson, 1969). The level of male and female aggression observed in *spinosus* and *horridus* was highly seasonable. In the August and June periods, the females defended territories while in February, they were passive. Although active in all three periods, the most active period of male aggression was the February period for these species. This indicated another problem for future work: why are females out of phase, aggressively, with the males? What factors controlled the onset of aggression in the two sexes? What were the levels of aggression in the field or was the behavior cycle a laboratory artifact? Hormone levels as influenced by light, temperature and reproductive cycles are almost certain to play a part. At the February observation, daylight was lengthening while the laboratory temperatures remained nearly constant. Possibly the increasing photoperiod stimulated the males, while the females were influenced by a different factor or showed a delayed reaction to the light.

Theoretically, it would seem advantageous for the agressive cycles of the sexes to be out of phase. When males were more aggressive in setting up territories and courting females, the females' aggressiveness was relatively low and probably indicative of greater tolerance or attentiveness to a courting male. However, in the enclosure, no copulations were observed in the spinosus group of Sceloporus, at any time; this was in marked contrast to smaller iguanids which readily mated in the enclosures. The females were more aggressive in the summer months, the period of egg-laying. Thus, two separate peaks of hormone levels can be postulated; the male's peak associated with territoriality, the female's peak associated with egg laying. In the Galapagos Marine Iguana, Amblyrhynchus, (Carpenter, 1965b) the cycle of aggression was clearly dyphasic with the males being highly aggressive and territorial earlier in the season and with the females' aggression being displayed during nesting.

One bias in interpreting relationships on the basis of observed social behavior was that most of the activity was restricted to a few dominant males. Thus, numerical data on interactions within and between species were heavily weighted to reflect the activity of a few individuals. An aberrant dominant could invalidate those results indicating behavioral relationships between species. Another variable was that the context of the interactions was not controlled--a hyperactive or hyperstimulated male might have reacted to stimuli (species or individuals) to which he normally would not respond.

Strong male dominance hierarchies developed in magister, horridus, spinosus, acanthinus, clarki and orcutti. All of these, except clarki are primarily rock or ground dwelling species. However, clarki is not entirely restricted to trees as it is found in terrestrial situations. Smith (1946) stated both magister and clarki are ubiquitous in habitat preference, but that clarki was found on trees in areas of overlap. Weak dominance hierarchies were established by strongly arboreal species melanorhinus and olivaceus, while very few interactions were seen in the arboreal edwardtaylori. Thus, the strongly arboreal lizards of the spinosus group of Sceloporus were not observed to form typical strong dominance hierarchies characteristic of enclosed lizard populations. Unlike the terrestrial species in which a dominance hierarchy was a phenomena of compressing and overlapping their primarily two-dimensional territories (Hunsaker and Burrage, 1969), the arboreal species with their vertical territories seemed incapable of compressing their territorial behavior into a mainly horizontally structured enclosure. Though several posts, a small dead tree and logs were placed in the enclosure, this apparently did not satisfy the arboreal requirements of these species. Blair (1960) reported that the arboreal *olivaceus* were restricted to one adult male per tree. *Sceloporus edwardtaylori* and *melanorhinus* appeared to be dispersed in this same way. However, terrestrial species taken in arboreal situations (*spinosus* and *horridus*) were also usually taken as one male per tree. Two hypotheses might explain the lack of behavior on the part of arboreal species: 1) a large vertical habitat is required for normal agonistic behavior to develop and 2) overcrowding could disrupt the development of normal agonistic behavior. Thus, the arboreal species of the *spinosus* group of *Sceloporus* might prove to be another exception to the gradation between territorial and hierarchial behavior of Hunsaker and Burrage (1969) besides the female behavior of *spinosus* and *horridus*. Lynn (1965) found that *Phrynosoma* did not form a hierarchy in an enclosure, but their behavior in the field did not suggest that they were actively territorial.

The hypothesis on the inhibition of arboreal species behavior should be examined in a large enclosure or in a field situation. Ideally, using two large similar sized enclosures, one could test the effect of sequentially adding conspecifics to an arboreal and terrestrial form of the *spinosus* group of *Sceloporus* to observe the effective change of social behavior with crowding. These enclosures should contain appropriate habitat, or better yet, be two different experiments and test the effect of sequential adding of lizards of both habitat types separately, in a horizontal habitat (rock) vs. a vertical one (large trees). Such an experiment should test the hypothesis of Hunsaker and Burrage (1969) on the gradation of social behavior that exists between territorial and hierarchial systems.

Observations of enclosured lizards can be quite useful in elucidating species relationships. All male members of a species will interact (if active) in forming an intraspecific peck order and initiating a high number of intraspecific courtships. Only one study besides Lynn (1965) has failed to support this statement. Bussjaeger (1967) had behavioral separation between Californian o. orcutti and o. tortigensis (o. orcutti from Tortuga Island, Gulf of California). They acted as separate species, ignoring each other. Because of the insular status of the latter and the clinal variation which existed on the mainland to the coloration type found on the island, Bussjaeger (1967) proposed that the island form be recognized as a separate subspecies.

There have been several reports of interactions between species and even genera within enclosures, especially if their morphology was similar. Above the intraspecific level, most interactions were between highest ranking males of each species; for example, the dominant male Callisaurus "picked-on" the dominant Cophosaurus (Clarke, 1965). Interaction of dominants has occurred frequently between closely related species. In this regard one should not consider solely the presence or absence of interaction but the degree of interaction.

Two species pairs of the spinosus group of Sceloporus stand out because of their numerous interactions: clarki-magister

(Bussjaeger, 1967) and *horridus*-*spinosus*. The former pair are sympatric in the northern part of their range, the latter completely allopatric. Both the above species pairs have been considered conspecific (Smith, 1939). A greater number of intraspecific interactions indicates their distinctiveness as species and one member of each pair demonstrated a strong intraspecific dominance and courtship preference (Table 14). At the same time, they did interact with one another. In the *spinosus*-*horridus* pair, the males of *horridus* showed a greater degree of differentiation than did males of *spinosus*. The latter were indiscriminate and interacted with *horridus* as if they were conspecific (Table 14).

Between some species, the lack of activity was more significant instead of the amount of activity. The uniform back members, *melanorhinus* and *edwardtaylori* ignored the striped line. The *formosus* group members, *asper* and *acanthinus* (Table 15) were non-entities in the enclosure with populations of *spinosus* and *horridus*.

Females of *spinosus* interacted with females of their own species and *horridus*, but not with *acanthinus* females. Females of *horridus* and *acanthinus* did not readily initiate interspecific interactions. Where males of *spinosus* were typically inactive and seemingly subordinated by the males of *horridus* the reverse was true for dominance in the females of these species.

Phylogeny

The earlier discussion of the biogeographical origin of the spinosus group of Sceloporus should be re-examined to test the validity of display-action-patterns (Table 20). This discussion is simplified in that the display-action-patterns are discussed as if they have been stable through time and only the main patterns are discussed. The basic display of the spinosus group of Sceloporus assumed to contain elements of display both from the clarki and magister lines--one similar to the present form of orcutti, lundelli and acanthinus. This is postulated on the basis that lundelli of the spinosus group and acanthinus of the formosus group were initial isolates from the pre-spinosus-formosus group ancestor east of the isthmus of Tehuantepec. One might expect these forms to have a primitive karyotype when they are examined. The trend of the display-action-patterns of the magister line agrees with previous trends of display-action-patterns in other genera. It also supports the present phylogenetic relationship of this line.

The display-action-patterns of the uniform line are inconclusive. The display of clarki is quite different from those of melanorhinus. These two species are also distinct in coloration. The displays of melanorhinus and edwardtaylori show basic similarities which seem to indicate a closeness that their coloration and karyotypes do not. Possibly, edwardtaylori is derived from melanorhinus karyotypically. The similarities of the uniform line apparently represent a complex group whose affinities are old and have been greatly modified.

In addition to interpreting the relationships of these species, the subspecific variation in the display-action-patterns

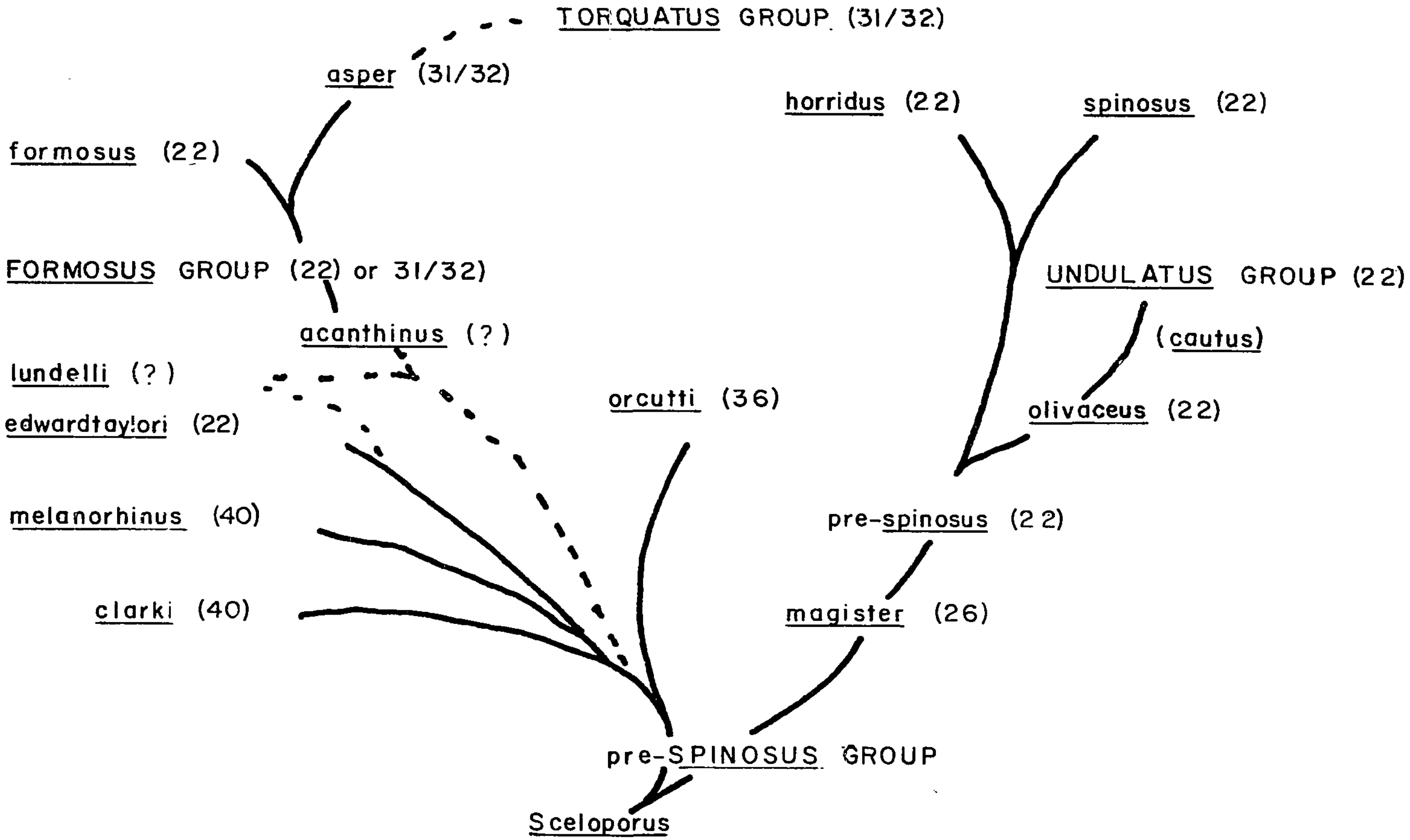

Fig. 20. Proposed phylogeny of the *spinosus* group of *Sceloporus*. Total capitals indicate species groups. Undetermined relationships are indicated by dotted line. Number in parentheses is diploid karyotype.

Table 20. Comparison of elements composing the display-action-patterns of the <u>spinosus</u> group of <u>Sceloporus</u> and some related forms.

			DISPLAY COMPONENTS													
	Dorsal color pattern: S=striped U=uniform	Habitat preference: T=terrestrial A=arboreal U=ubiquitous (lower case letter = 2nd pref.)	Single Units				Multiple Units		Number of Introductory Units				Repeated Units			
							Double	Triple								
Species			Peaked	short	Median	long			2	3	4	5	1	2	3	4
horridus	S	T-u	?	X	X					X				X		
spinosus	S	T	X	X	X	X				X			X			
magister	S	T	X	X	X					X			X			
olivaceus	S	A		X			X			X			X			
clarki	U	A-u		X			X			X			X			
orcutti	U	T		X	X		X	X		X	X		X			
edwardtaylori	U	A		X	X				X						X	
melanorhinus	U	A			X						X					X
lundelli	U	A	X				X	X			X		X			
acanthinus	U	U	X	X			X			X				X		
asper	U	A	X				X					X	X			
undulatus	S	T		X						X				X		
torquatus group	U	T		X	X					?			X			

of clarki confuse the phylogenetic interpretation. The display of c. boulengeri is distinct from c. clarki (Fig. 19). The latter has the most variable display-action-patterns of any member of the spinosus group of Sceloporus. The displays of c. clarki have apparently undergone character displacement so that they are distinct from the uniform single unit displays of sympatric magister. The display of c. boulengeri, being composed of single units, approaches the ideal primitive display for the uniform back line. On the basis of the displays alone, it seems as if clarki is primitive to two lines of evolution--one giving rise to orcutti, the other giving rise to melanorhinus-edwardtaylori.

Some further comments on subspecific relationships are in order. Phelan and Brattstrom (1955) diagrammed the subspecies phylogeny of the magister group. I have no behavioral evidence to document his phylogeny as the displays of the subspecies, m. transversus, m. uniformis, and m. magister, are the same. The subspecies of horridus are apparently recently derived from one stock as indicated by their similar displays and the fact that two display patterns are fixed in all three subspecies. Because their displays were identical, they have similar femoral pore counts as well as more similar ventral coloration, the subspecies of h. oligoporus and h. albiventris are evidently more closely related to each other than to h. horridus. The latter subspecies is closer to spinosus than the other two, as evidenced by its distribution and its deeper ventral coloration. Evolution in the subspecies of spinosus is probably a straight line from the plateau of Oaxaca.

The two subspecies, *s. apicalis* and *s. caeruleopunctatus*, seem similar; to the point that the subspecific status of *s. apicalis* seems to be splitting fine hairs. The displays of the subspecies of *spinosus* support the earlier diagram of the relationships within this species (Fig. 2).

The relation of *cautus* and *olivaceus* and the *undulatus* group of *Sceloporus* has been questioned. Hall's data indicated that these two species were the same and limited data on their displays indicates that they are similar. If one accepts that they are synonoms, then *olivaceus* (*cautus*) would be the connecting link between the *spinosus* and *undulatus* groups. This would also mean that *olivaceus* is not strictly arboreal. It may indicate that *cautus* secondarily invaded the central plateau to overlap the distribution of *spinosus*.

The status of *lundelli* is questionable. Smith (1939) believed that it was close to *acanthinus*. Its display-action-pattern was between *acanthinus* and *orcutti*, but the pattern was based on only one female. More data are needed to establish this species relationship. At present it should be left in the *spinosus* group, although it appears to be closer to the *formosus* group. Its derivation from the *spinosus* group is problematical; it could be derived from the *clarki* line at the top of the tree or since its displays appears similar to *orcutti*, near the base of the tree. If its karyotype was 36, I would favor the primitive hypothesis near *orcutti*. If its karyotype was 22, I would favor the derived hypothesis.

In summary, displays of the spinosus group provides insight into closely related species and relationships can be ascertained between many forms; but more displays need to be determined to ascertain the usefulness within other species groups. At the present time, the displays cannot be used to define the spinosus group of Sceloporus although subspecies group complexes within it can be identified. The greatest use of the display-action-patterns appears to be at the species and subspecies levels.

CHAPTER VII

SUMMARY

The present study was undertaken to describe the aggressive displays and social behavior of the spinosus group of Sceloporus. It was hoped that the behavior could be used to test the phylogenetic significance of the display. The study was done from April 1966 to July 1969.

1. Display-action-patterns were determined for all species of the spinosus group of Sceloporus and some related species. For each species, sample size and number of localities sampled varied greatly.

2. Each species was characterized by one or a series of distinct display-action-patterns which were distinct for that species.

3. The displays of horridus were unique in that individuals performed two distinct display-action-patterns at random. These two patterns were characteristic for each subspecies of horridus.

4. Geographic (subspecific) variation was seen in horridus and spinosus. Samples from other species were taken from a too restricted geographic range to indicate geographical variation.

5. The most distinct lizard in both coloration and

display-action-pattern was melanorhinus.

6. Strictly arboreal lizards of the spinosus group of Sceloporus were characterized by:

   a) slower, distinctive units composing the display-action-pattern.

   b) weak or no dominance hierarchy exhibited in the enclosure.

7. The ubiquitous or terrestrial lizards of the spinosus group of Sceloporus were characterized by:

   a) rapid display-action-patterns of similar single units whose cadence increased as the display ended.

   b) strong dominance hierarchies formed in an enclosure.

8. Sceloporus cautus was considered closely related to olivaceus, but not enough data was collected to decide on their apparent synonymy with olivaceus.

9. Sceloporus acanthinus acanthinus and a. lunaei were recognized on the basis of social behavior as subspecies of acanthinus, thus following the taxonomy of Stuart (1953).

10. The display-action-patterns appeared to be useful as another character to compare phylogenetic status within the species groups and among closely related groups. The phylogenetic trend in the displays of the spinosus group appeared similar to those composed for other genera of iguanids.

11. Social behavior was observed at four different periods:

June 1966, September 1968, February and June, 1969.

12. On the basis of inter- and intraspecific competition, two closely related species pairs were identified: horridus-spinosus and magister-clarki.

13. Two species of the formosus group of Sceloporus (asper and acanthinus) were treated as non-entities in the enclosures by members of the spinosus group, thus emphasizing their distinctness.

14. Literature and data of other researchers were summarized on herpetogeny of Sceloporus in Mexico and karyotypes of the spinosus group of Sceloporus.

15. Behavioral data obtained in this study was interpreted on the basis of karyotypes and current ideas on the herpetogeny of Mexico were used to construct a new phylogeny for the spinosus group of the Sceloporus.

16. Several changes in the herpetogeny of the spinosus group were proposed:

a) Sceloporus orcutti is definitely primitive and close to the main line of the spinosus group of Sceloporus.

b) Sceloporus olivaceus adapted to trees secondarily after speciating from the main stem.

c) The present phylogenetic relations of the striped back species are supported while the relations of the uniform back line and the formosus group are unclear.

17. Sceloporus acanthinus is definitely in the formosus group and was found to be ovoviviparous.

18. The species group status of lundelli was questionable, but should be retained as a primitive spinosus group type until more specimens can be observed.

19. Social interactions of enclosed populations of spinosus and horridus were followed in three periods: September, 1968; February 1969 and June 1969.

20. Males of both species set up dominance hierarchies in all three enclosures. The males of horridus were most active in the February period. Females of these two species set up territories and defended sites from one another in September 1968 and June 1969, but not in February 1969. One dominant female had free access to the entire enclosure.

21. Hormonal control mechanisms were suggested for explaining the varying levels of aggression seen in the sexes of spinosus and horridus.

22. Some of the more interesting problems for future research include studies on:

a) the species group status of lundelli.

b) a competition between the two species in the field, melanorhinus and horridus, at Colima, Colima, Mexico.

c) geographical variation in the displays of the spinosus group.

d) The effects of crowding on an arboreal _spinosus_ group species.

e) The cyclic nature of aggression in the species, _spinosus_ or _horridus_.

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APPENDIX I

Table 21. Individual statistics on lizards collected for study.

Sex	Color	Toe Mark	Length (mm)		Weight (g)	Locality
			s-v	total		
Sceloporus edwardtaylori						
F	yy	Kj	112	261	67.8	25
M	yr	Ki	108	254	61.0	25
M	yy	Lj	104	252	46.3	26
M	yb	Kf	85	218	27.1	25
F	yr	Kg	93	204	33.0	25
M	yg	Ke	88	220	26.9	25
M	yo	Kd	83	172	22.3	25
M	yry	Kc	77	155	16.7	25
M	ywy	Kb	75	180	14.9	25
F	yw	Kl	78	99	17.2	25
F	yb	Km	73	182	15.4	25
M	yy	Gi	101	231	41.5	31 (5)
M	yr	Gj	95	198	37.35	31 (5)
M	yw	Hi	107	132	38.92	32 (6)
M	yg	Hj	96	223	34.15	32 (6)
M	yb	Gl	86	189	26.54	31 (5)
F	yy	Gm	106	210	37.53	31 (5)
F	yr	Go	102	238	34.6	31 (5)
F	yw	Gp	82	130	20.05	31 (5)
F	y	Gq	35.5	77	1.42	31 (5)
M	b	Gr	38	50	1.52	31 (5)
M	y	Gs	34	78	1.46	31 (5)
M	r	Gt	36	43	1.73	31 (5)
M	-	Hl	31	66	0.7	32 (6)
Sceloporus asper						
F	pp	b	61	71	6.22	33
F	-	a	26.5	54	--	33
F	py	aj	64	100	8.55	33
M	pp	ai	75	161	11.29	33
Sceloporus melanorhinus calligaster						
M	gb	Ef	94	230	31.8	14
M	gg	Ej	83	192	18.3	14
M	gr	Eg	82	210	18.4	14
M	gy	Eh	70	164	13.0	14
F	gr	Lj	83	201	21.3	16
F	gy	Ei	74	167	19.2	14
F	gg	Ea	81	183	18.4	14

Table 21, cont'd.

Sex	Color Mark	Toe Mark	Length (mm)		Weight (g)	Locality
			s-v	Total		
Sceloporus melanorhinus calligaster						
F	gb	j	86	183	23.35	36 (14)
M	go	i	93	227	26.85	36 (14)
M	gwg	h	84	201	21.07	35
M	gbg	g	90	180	22.43	35
M	gg	f	87	189	20.09	35
F	g(ydot)	e	76	159	14.82	33
M	pgp	d	77	175	12.77	33
M	pgr	c	74	134	11.89	33
M	gb	aj	87	215	24.8	36 (14)
M	gr	ai	87	170	25.67	36 (14)
M	gyg	ah	86	190	18.38	36 (14)
F	gw	ag	91	182	26.6	36 (14)
M	grg	af	93	111	24.63	36 (14)
M	gy	ae	91	215	29.18	36 (14)
M	gog	ad	82	193	17.89	35
F	gy	ac	78	179	21.30	37
F	--	ab	--	---	---	37
Sceloporus melanorhinus stuarti						
M	gy	i	104	177	43.5	45
Sceloporus horridus albiventris						
M	wbw	Aj	82	224	22.68	10
F	wr	Bhl	81	191	21.05	11
M	wb	Bik	91	210	21.03	11
M	--	j	69	111	--	33
M	bw	i	102	237	40.0	33
M	bo	h	76	205	19.6	33
F	--	g	--	---	--	33
F	--	f	69	141	--	33
M	bg	e	77	167	14.40	33
M	bbb	d	77	207	11.37	33
M	--	c	63	170	--	33
M	by	b	97	183	34.28	33
M	bwb	a	78	209	17.0	33
M	--	aj	70	129	--	33
M	--	ai	60	90	--	33
F	by	ah	65	176	10.45	33
M	brb	ag	73	198	14.66	33
F	br	af	71	184	11.84	33
F	bb	ae	69	132	11.90	33
M	--	ad	103	238	--	33
M	br	ac	98	127	37.31	33
M	bw	ab	90	219	34.68	33

Table 21, cont'd.

Sex	Color Mark	Toe Mark	Length (mm)		Weight (g)	Locality
			s-v	Total		
Intergrades: *S. h. albiventris* - *S. h. oligoporus*						
M	gg	j	83	205	--	52
M	wgw	Cgm	83	217	24.34	12
M	wrw	Cik	84	220	24.20	12
M	wr	Chl	90	239	34.4	12
Sceloporus horridus oligoporus						
M	wyw	Dfn	88	227	30.90	13
M	wo	Dfm	79	165	20.4	13
M	wg	Dik	85	134	25.7	13
M	wy	Dl	99	259	42.62	13
F	wy	Lj	87	194	31.22	15
M	rr	Hj	89	143	30.4	22
M	rw	Hi	94	204	43.1	22
F	rr	Hg	85	184	26.2	22
F	rw	Hf	85	167	24.8	22
M	pdbo	k	84	235	19.51	34
M	pdbb	kj	105	224	39.27	34
F	pdbo	ki	82	155	23.14	34
M	pdbg	kh	82	125	20.6	34
M	pdbw	kg	105	239	46.89	34
M	pdby	kf	94	235	35.85	37
M	pdbr	ke	102	227	38.33	37
F	pdbr	kd	87	129	28.69	37
F	pdbb	kc	86	161	26.90	37
F	pdby	kb	86	220	28.14	37
F	pdbw	l	92	202	32.43	37
F	pdbg	lj	76	192	17.35	37
M	pdbp	li	84	213	--	40
F	pdbp	ghi	83	208	--	40
Sceloporus horridus horridus						
M	ry	Ej	107	273	49.3	21
M	rb	Ei	99	232	45.4	21
M	rg	Eh	90	169	26.5	21
M	ro	Eg	92	191	29.0	21
F	ry	Ef	82	210	21.7	21
F	rb	Ed	85	227	24.7	21
F	rg	Ec	91	137	23.7	21
M	--	I	43	108	2.37	52

Table 21, cont'd.

Sex	Color Mark	Toe Mark	Length (mm) s-v	Length (mm) Total	Weight (g)	Locality
		Sceloporus horridus horridus				
M	ry	Cd	82	226	25.16	29
M	rb	Bc	83	184	20.16	28
M	rg	Ab	80	199	20.63	27
M	ro	Bd	73	200	15.48	28
M	ryr	Bo	79	197	18.47	28
F	rr	Bf	75	199	17.52	28
F	ryb	Ac	74	179	13.95	27
F	rw	Bg	75	197	14.6	28
F	rg	Bi	78	197	15.06	28
F	ro	Bj	70	190	13.6	28
F	ryr	Bk	69	189	12.77	28
F	rgr	Bl	70	121	12.35	28
F	rbr	Cf	67	183	11.47	29
F	ror	Bm	68	178	9.96	28
F	ryg	Bn	66	150	8.98	28
		Sceloporus spinosus spinosus				
M	lby	Ap	107	134	43.2	3
M	lbw	AEg	106	122	49.4	4
M	lbr	AEf	87	186	28.6	4
F	lby	aK	83	149	22.7	2
F	lbw	eK	45	89	3.0	2
F	lbr	fK	53	123	2.5	2
M	bg	Rj	110	224	55.9	17
M	br	Rp	108	214	52.5	17
M	by	Rqsg	84	180	25.0	17
M	bw	Ri	90	204	27.5	17
F	br	Rgk	80	183	23.9	17
F	bg	Rh	84	196	22.8	17
F	bw	Rg	73	169	17.2	17
F	bo	Rf	71	131	9.2	17
F	bb	Cj	75	187	18.0	20
M	bb	Ci	119	258	77.8	20
F	by	Aj	99	133	43.3	18
F	brb	Ch	84	192	22.5	20
M	brb	Cg	80	187	19.5	20
M	byb	Cf	78	188	17.9	20
M	bgb	Ce	75	179	16.8	20
F	byb	Bj	75	187	17.9	19
F	bgb	Cd	76	178	18.2	20

Table 21, cont'd.

Sex	Color Mark	Toe Mark	Length (mm)		Weight (g)	Locality
			s-v	Total		
		Sceloporus spinosus caeruleopunctatus				
M	sw	Ji	98	171	39.3	24
M	sr	Jh	92	215	34.5	24
M	sy	Jg	96	220	33.6	24
M	sgwg	Jf	95	188	34.4	24
M	sb	Je	90	209	26.5	24
M	so	Jd	79	101	22.4	24
F	sw	Jc	91	202	30.5	24
F	sr	Jb	90	205	32.1	24
F	sy	Ja	82	184	20.0	24
F	wr	Ef	53	116	4.45	30
F	wo	j	71	168	16.48	38
F	ww	i	88	155	29.68	38
F	wrg	h	64	145	10.79	38
F	wg	g	73	89	11.43	38
M	ww	f	100	231	36.44	38
F	wwg	e	64	101	10.54	38
F	wb	d	92	197	33.08	38
M	wr	c	87	194	22.21	38
F	wy	b	90	173	27.10	38
F	wbg	a	58	72	5.65	38
F	wr	aj	88	176	29.30	38
M	ywb	ai	92	213	28.18	38
M	wb	ah	74	128	14.36	38
		Sceloporus spinosus apicalis				
M	ywo	ag	102	261	43.60	39
M	yww	af	91	114	29.68	39
M	ywr	ae	100	145	33.89	39
F	ywr	ad	82	156	27.71	39
F	yww	ac	85	204	26.2	39
F	ywb	ab	75	155	16.32	39
M	ywy	k	63	113	11.92	39
F	--	kj	--	--	--	39
		Sceloporus clarki boulengeri				
M	rr	ne	115	260	67.0	50
M	ry	nc	125	253	78.8	50
F	rr	ng	82	193	23.0	50
F	ry	nf	85	208	23.3	50
M	o	a	92	186	36.7	33
M	b	b	96	219	39.26	33

Table 21, cont'd.

Sex	Color Mark	Toe Mark	Length (mm)		Weight (g)	Locality
			s-v	Total		
Sceloporus clarki clarki						
M	rw	kg	108	236	42.7	52
F	rw	kd	99	189	25.2	52
F	rg	l	100	210	25.2	52
M	rg	ly	96	226	33.1	52
M	ryw	lh	107	238	43.1	52
M	rylb	lg	88	207	24.6	52
M	ryr	lf	84	196	20.3	52
M	rlb	hl	118	275	44.5	52
Sceloporus magister magister						
M	ww	ag	115	260	59.6	52
M	wo	lj	116	261	46.1	52
M	wy	li	114	224	53.1	52
M	wr	lh	112	198	49.0	52
M	wg	lg	102	203	41.2	52
Sceloporus magister uniformis						
M	blo	A	81	184	20.3	46
F	blo	B	83	194	21.8	46
F	blw	C	85	194	24.7	47
F	blb	D	66	79	11.2	47
Sceloporus orcutti orcutti						
F	gw	h	88	196	25.3	52
Sceloporus orcutti tortugensis						
M	y	-	66	123	12.66	(hatched)
M	yo	aeI	100	214	33.2	51
M	yw	eI	83	179	21.7	51
M	ybl	bI	93	199	24.8	51
M	yr	hIk	88	192	--	51
M	yy	I	90	200	22.9	51

Table 21, cont'd.

Sex	Color Mark	Toe Mark	Length (mm)		Weight (g)	Locality
			s-v	Total		
			Sceloporus olivaceus			
M	oo	j	68	109	9.3	7
M	olb	i	64	97	10.0	8
F	olb	h	62	165	9.0	8
F	oo	g	99	139	47.6	9
F	or	f	51	81	3.9	8
M	oy	e	58	153	7.2	8
F	ow	d	77	153	14.3	8
M	ow	c	70	188	12.3	8
M	or	b	62	169	9.9	9
M	owr	a	80	205	19.8	8
F	oyo	aj	96	244	34.3	8
M	owlb	ai	79	184	24.6	8
M	owy	ah	84	220	24.0	8
M	owg	ag	80	197	17.7	8
F	og	af	61	156	7.3	8
F	oyr	ae	58	158	7.9	8
M	og	ad	60	98	6.8	8
M	oyg	ac	62	167	7.3	8
F	owg	ab	66	181	11.1	8
F	owlb	k	88	226	26.2	8
F	owo	kj	97	244	45.2	8
F	ogo	ki	91	241	33.4	8
F	owy	kh	87	219	24.5	8
F	oylb	kf	67	103	10.1	8
M	oyr	ke	70	166	13.1	8
M	oylb	kd	72	188	13.7	8
M	oro	kc	90	225	28.7	8
M	ogo	kb	92	227	27.7	8
F	oro	l	92	230	33.7	8
M	oblo	lj	93	137	37.1	8
M	oyo	li	94	234	30.9	8
M	owo	lh	92	175	33.8	8
F	olbo	lg	104	247	41.6	8
			Sceloporus cautus			
M	dbw	AGh	60	72	9.5	5
M	dby	AGf	55	69	5.5	6

Table 21, concl'd.

Sex	Color Mark	Toe Mark	Length (mm) s-v	Length (mm) Total	Weight (g)	Locality
			Sceloporus acanthinus acanthinus			
M	yy	Cd	89	207	27.5	41
M	yb	Ce	88	189	26.2	41
F	yy	Cb	83	177	18.0	41
F	yb	Cg	57	123	6.8	41
F	yr	Ch	56	126	6.7	41
F	yw	Ci	53	115	5.5	41
F	y	Cj	50	106	4.3	41
			Sceloporus acanthinus lunaei			
M	oo	De	87	186	23.0	42
F	oo	Df	81	175	24.2	42
F	ob	Dg	66	140	--	42
F	oy	Dh	55	122	5.6	42
M	ww	Fg	68	150	17.5	43
M	wy	Fh	56	120	6.6	43
F	ww	Fi	49	72	4.2	43
F	wy	Hi	53	118	4.4	44
			Sceloporus lundelli gaigea			
F	bly	KLMN	95	184	25.7	48

APPENDIX II

Table 22. Collection data of lizards studied.

Map No.	Coll. Date	Locality	Anogram of species collected *spinosus* group	 other	Habitat Description and collection data
1	3/29/66	Pyramid at Cholula, Puebla, Mexico	*S.s.s.*	--	Edge of town, brushy wooded hillside with boulders and rock wall.
2	3/29/66	SSW of Apizaco on new road to Tlaxcala, Mexico	*S.s.s.*	*S.t.t.*	Edge of adobe village--barren, arid, boulder-strewn hillside, fence rows of agave cactus. *S.s.s.* associated with bases of maguey (*Agave*) and large boulders. S.t.t. associated with crevices of cliffs.
3	3/30/66	28 km NW of Pachuca, HW 85, Hidalgo, Mexico	*S.s.s.*	--	A gorge with small stream, sheer rock cliffs with clumps of *Agave lechugilla*, pepper trees (*Schinus molle*), short grasses and other cactus.
4	4/1/66	16 km SW San Luis Potosi, Hw 86, S.L.P., Mexico	*S.s.s.*	--	Goat-denuded rocky hillside of low boulders, scattered trees--almost vegetationless--low scrub oaks, *Quercus*, sp., in protected areas.

Table 22, cont'd.

Map No.	Coll. Date	Locality	Anogram of species collected		Habitat Description and collection data
			spinosus group	other	
5	4/1/66	18 km N of Matchuala, Hw 57, S.L.P., Mexico	*S.c.*	--	Arid gravelly area--scattered creosote bush (*Larrea divaricata*).
6	4/1/66	20 km N of San Roberto, Nuevo Leon, Mexico	*S.c.*	--	Same as 5.
7	4/25/66	16 km S, San Marcos, Tex., U.S.A., Hw 81	*S.o.*	--	Grove of oak trees.
8	6/10/66	Fort Worth Texas, U.S.A. Will Rogers Colliseum Botanical Gardens Rockwood park	*S.o.*	*E.l.*	Park areas of city with large oak, elm and mesquite trees, shrubs nearby and grassy understory. *S.o.* always on trees.
9	6/12/66	Oak Park Golf Course, Dallas, Texas, U.S.A.	*S.o.*	--	Parkland. See Site 8.
10	3/26/67	35 km E, Ixtlan del Rio, Hw 15, Jalisco, Mexico	*S.h.a.*	*S.n.* *C.s.* *U.b.*	Xeric, lava boulder strewn hillsides, candellabra cactus, prickle nut trees (*Guazuma ulmifolia*) and various *Acacia* sp.

Table 22, Cont'd.

Map No.	Coll. Date	Locality	Anogram of species collected		Habitat Description and collection data.
			spinosus group	other	
11	3/26/67	46 km W. Ixtlan del Rio, Hw 15, Jalisco, Mexico	*S.h.a.*	*S.n* *C.s.*	Loose rock wall--weedy fields. Same trees as area 10, but most natural vegetation removed.
12	3/27/67	13 km N, Cocula, Hw 80, Jalisco, Mexico	*S.h.a.*	*S.d.d.* *U.b.*	Isolated boulder strewn hillside with scattered scrub trees, scattered grasses. *S.h.a.* on top rocks, *S.d.d.* in crevices (10 in one crack), *U.b.* in trees.
13	3/27/67	35 km N, Union de Tula, Hw 80, Jalisco, Mexico	*S.h.a.*	--	Cleared farm & pastureland--*S.h.a.* associated with cement fence posts, spiny brush in ditches and large isolated trees and large rocks. Only narrow strips of habitat.

Table 22, Cont'd.

Map No.	Coll. Date	Locality	Anogram of species collected		Habitat Description and collection data.
			spinosus group	other	
14	3/28/67	10 km E, Manzanillo, Hw 200, Colima, Mexico	*S.m.c.*	*U.b.* *S.p.* *C.*-	Dry sandy stream bed. S.m.c. associated exclusively with yellow grass trees (*Astianthus viminalis*) which occurred in clumps in dry sandy wash.
15	3/28/67	16 km S, Colima, Hw 10, Colima, Mexico	*S.h.o.*	*S.p.* *U.sp*	Thorn forest--lizards on candelabra cactus in dry arroyo.
16	3/29/67	96 km S, Uruapan, Hw 37, Michoacan, Mexico	*S.h.o.*	*E.c.* *S.p.* *U.g.*	Very arid with thorn trees.
17	3/30/67	5 km S, San Luis Potosi, Hw 80, S.L.P., Mexico	*S.s.s.*	--	*S.s.s.* on cement fence post near clumps of mesquite trees (*Prosopis*).
18	8/14/67	Balneario Tzindejeh, Tasquillo, Hw 85, Hidalgo, Mexico	*S.s.s.*	--	Cultivated river valley--*S.s.s.* on wooden fence posts near brush, trees and downed trees.

Table 22, Cont'd.

Map No.	Coll. Date	Locality	Anogram of species collected *spinosus* group	other	Habitat Description and collection data
19	8/14/67	6 km S, Tasquillo, Hw 85, Hidalgo, Mexico	*S.s.s.*	--	Arid brush-land, gravelled, small mesquite trees and line of road-side rocks left by grader.
20	8/14/67	16 km S, Ixmiquilpan, Hw 85, Hidalgo, Mexico	*S.s.s.*	--	In roadside shrubs, rocks and Yucca, which lined the road as border to fields and pastureland.
21	8/16/67	37-65 km S, Cuernavaca, Hw 95, Morelos, Mexico	*S.h.h.*	*A.*sp	Valley of irrigated farmland. S.h.h. on 40' salt cedars (*Tamarix* sp), other trees and block fence posts.
22	8/18/67	13 km E, Zihuatanejo, Hw 200, Guerrero, Mexico	*S.m.c.* *S.h.o.*	*U.*sp	In yellow grass trees (*A. viminalis*) bordering dry stream.
23	8/19/67	33 km W, Izucar de Matamorus Hw 140, Puebla, Mexico	*S.h.h.*	*U.*sp	High plain east of Cuernavaca--scattered lava boulders in fenced pasture land--lizards seen on rocks, fence and telephone poles.

Table 22, Cont'd.

Map No.	Coll. Date	Locality	Anogram of species collected: *spinosus* group	Anogram of species collected: other	Habitat Description and collection data
24	8/20/67	3-16 km S of Oaxaca, Hw 175 Oaxaca, Mexico	*S.s.c.*	--	Cleared cultivated field and pastures with trees scattered in fields, along streams and bordered. *S.s.c.* found on pepper trees, yellow grass trees and unknown thorn tree with many natural cavities (previously reported to be solely a terrestrial species).
25	8/21/67	10 km S, Tehuantepec Hw 185, Oaxaca, Mexico	*S.e.*	*E.q.* *S.s.* *U.* sp *P.* sp *A.* sp	Both in open scrub forest with scattered large trees, cleared for farming and grazing. The coastal site (25) is more xeric, flatter and open. It is primarily scrubby thorn trees with scattered large trees and hedgerow type thickets.
26	8/21/67	5 km N, jct 190 & 185, Oaxaca, Mexico	*S.e.*	Same as 25	Has larger trees and much more vegetation, forming a closed forest (compared to 25). Here & at 25, *S.e.* found only on trees.

Table 22, Cont'd.

Map No.	Coll. Date	Locality	Anogram of species collected		Habitat Description and collection data
			spinosus group	other	
27	3/22/68	13 km S, Cuernavaca, Hw 75, Morelos, Mexico	*S.h.h.*	*U.* sp	Roadside thorn trees, salt cedars and willows with lizards on latter two trees.
28	3/23/68	16 km SE Cuernavaca, Hw 115, Morelos, Mexico	*S.h.h.*	*C.* sp *U.* sp	Heavily grazed fields and pastures with many lava rocks. *S.h.h.* taken off loose rock walls and piles as well as scattered trees.
29	3/23/68	6 km SE Cuatla, Hw 140 Morelos, Mexico	*S.h.h.*	*U.b.*	Flat plain. Lizards on scattered small lava boulders, wooden fence posts and telephone poles, similar to site 23.
30	3/24/68	47 km NW Oaxaca, Oaxaca, Mexico	*S.s.c.*	*S.j.* *S.m.o.*	One *S.s.c.* found in road-side cut by boulders in oak forest.
31	3/24/68	5-14 km S. Tehuantepec, Hw 185, Oaxaca, Mexico	*S.e.*	*U.b.* *S.s.*	Same as site 25.
32	3/25/68	5 km N jct 185-190, Oaxaca, Mexico	*S.e.*	*P.* sp *S.s.* *C.s.*	Same as site 26.

Table 22, Cont'd.

Map No.	Coll. Date	Locality	Anogram of species collected		Habitat Description and collection data
			spinosus group	other	
33	5/7/68	17-36 km E, Tepic, Hw 15, Nayarit, Mexico	*S.h.a.* *S.c.b.* *S.m.c.*	*U.o.* *S.s.* *S.n.* *S.u.* *C.p.* *A.n.* *Cn.s.* *Eu.* sp	The lizards, *S.h.a.*, was most abundant in boulder strewn pasture land near road where shrub vegetation was plentiful. Also seen in Tepic, on rock walls and trees.
34	5/20/68	10 km N. Tecolotlan, Hw 80, Jalisco, Mexico (Three areas in 16 km stretch)	*S.h.o.*	--	a) Road cut--associated with boulders on road cut in pine-oak forest. b) Rio Pichote--overgrown rock wall with *Opuntia*, candelabra cactus and yellow grass trees. c) Rio San Jose--cleared parkland & stream bed, only on yellow grass trees.
35	3/20/68	Rio Maralasco, 13 km E, Barra de Navidad	*S.m.c.*	--	Similar to site 14.
36	4/21/68	10 km E, Manzanillo, Colima, Mexico	*S.m.c.*	*U.* sp	Same locality as 14.

Table 22, Cont'd.

Map No.	Coll. Date	Locality	Anogram of species collected: spinosus group	Anogram of species collected: other	Habitat Description and collection data
37	4/21/68	4 km S, Colima, Colima, Mexico	S.m.c. S.h.o.	U. sp	All were found on scattered medium to large road-side thorn trees.
38	5/24/68	4-40 km transect N of Ejutla, Hw 175, Oaxaca, Mexico	S.s.c.	--	Lizards seen on isolated rocks near very low Acacia. Vegetation is scrubby and quite low.
39	5/24/68	8 km S Miahuatlan, Hw 175 Oaxaca, Mexico	S.s.a.	--	Rocky arid land with scrub oak trees of less than 3 m., isolated trees and yucca fences. S.s.a. were found on rocks, trees and yuccas.
40	8/12/68	Oklahoma University, Hacienda, Colima, Mexico	S.h.h.	--	Collected by Dr. C. C. Carpenter.
41	4/1/69	10 km SW Retalhuleu, Hw 95, Guatemala	S.s.a.	A. sp	Taken exclusively from 60' tall willow-like trees, extensive marsh-grass below--edge of wet weather swamp.

Table 22, Cont'd.

Map No.	Coll. Date	Locality	Anogram of species collected		Habitat Description and collection data
			spinosus group	other	
42	4/3/69	Salamá, 2-5 km SE Salamá, Guatemala	*S.a.l.*	*B.* sp *S. v.*	*S.a.l.* taken from roadside trees, pile of dead overturned trees.
43	4/4/69	25 km W Jutiapa, Hw CA1 Guatemala	*S.a.l.*	--	Roadside lava boulders, small trees, fence posts.
44	4/4/69	Jalapa, Guatemala	*S.a.l.*	--	East edge of town, associated with boulders and fence posts.
45	4/6/69	3 km N Cuauhtemoc, Hw 190 Chiapas, Mexico	*S.m.s.*	--	In dry wash next to road on large deciduous trees.
46	5/11/69	4 km W, Silver Springs, Utah, U.S.A.	*S.m.u.*	--	Donated by Fenton R. Kay, Univ. Utah.
47	6/2/69	41 km N, Tonopah, Utah	*S.m.u.*	--	Same as 46.
48	5/-/69	Progresso, Yucatan, Mex.	*S.l.g.*	--	Donated by Jerry Penner, Univ. Okla.
49	/66	unknown - pet supply	*S.c.c.* *S.m.m.*	--	Oklahoma City Zoo, Jaren Horsley

Table 22, Cont'd.

Map No.	Coll. Date	Locality	Anogram of species collected		Habitat Description and collection data
			spinosus group	other	
50	/65	N, Mazatlan, Hw 15, Sinaloa, Mexico	*S.c.b.*	--	Donated by John Lannon, Jr.
51	8/ /64	Tortuga Island, Gulf of California, Mexico	*S.o.t.*	--	Arid volcanic island with scattered cactus.
52	--	--	--	--	Various reptile dealers, no data

Table 22, Cont'd. (Anogram of species collected, *spinosus* group column)

S.c.c. = *Sceloporus clarki clarki*

S.c.b. = *Sceloporus clarki boulengeri*

S.e. = *S. edwardtaylori*

S.h.a. = *S. horridus albiventris*

S.h.h. = *S.h. horridus*

S.h.o. = *S.h. oligoporus*

S.s.a. = *S. spinosus apicalis*

S.s.s. = *S.s. spinosus*

S.m.c. = *S. melanorhinus calligaster*

S.m.s. = *S.m. stuarti*

S.c. = *S. cautus*

S.o. = *S. olivaceus*

S.m.m. = *S. magister magister*

S.m.u. = *S.m. uniformis*

S.a.l. = *S.a. lunaei*

S.a.a. = *S.a. acanthinus*

S.l.g. = *S. lundelli gaigea*

S.o.t. = *S.o.t.* (*S.o. orcutti* from Tortuga Island)

S.s.c. = *S.s. caeruleopunctatus*

Table 22, cont'd. (Anogram of species collected, "other" column).

Am. sp. = Amevia sp.

A. sp. = Anolis sp.

A.n. = A. nebulosus

B. sp. = Basciliscus sp.

Cn. s. = Cnemidophorus sackii

C. sp. = Ctenosaura sp.

C.p. = C. pectinata

C.s. = C. similis

E.c. = Enyaliosaurus clarki

E.q. = E. quinquecarinatus

Eu. sp. = Eumeces sp.

Eu. l. = E. laticeps

P. sp. = Phyllodactylus sp.

S.d.d. = Sceloporus d. dugesi

S.j. = S. jalapae

S.m.o. = S. mucronatus omiltemanus

S.n. = S. nelsoni

S.p. = S. pyrocephalus

S.s. = S. siniferus

S.t.t. = S.t. torquatus

S.u. = S. utiformis

S.v. = S. variabilis

U. sp. = Urosaurus sp.

U. b. = U. bicarinatus

U.g. = U. gadovi

U.o. = U. ornatus

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