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# Contributions in Biology and Geology

Number 18  
May 14, 1978

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by Charles C. Carpenter  
University of Oklahoma

MILWAUKEE  
PUBLIC  
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Milwaukee Public Museum Press  
Published by the order of the Board of Trustees  
Milwaukee Public Museum  
Accepted for publication January 19, 1978.

**REVIEW COMMITTEE FOR THIS PUBLICATION:**  
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# COMPARATIVE DISPLAY BEHAVIOR IN THE GENUS *SCELOPORUS* (IGUANIDAE)

CHARLES C. CARPENTER

University of Oklahoma  
Department of Zoology  
Norman, Oklahoma 73019

## Abstract

The large lizard genus *Sceloporus* (Iguanidae) ranges widely throughout the Nearctic from New England to Panama, inhabiting a broad spectrum of habitats to over 3000 meters. Males exhibit aggressive behaviors involving posturing with pushups and head bobbing movements which appear in species-characteristic sequential display-action-patterns.

The aggressive behaviors of 42 species of *Sceloporus* (divided in 15 subgroups) were observed and photographed on cine film in large enclosures in Oklahoma. The sample sizes used varied between species. Categories for comparing the display movements through the time were site, orientation, posture, type of movements, sequences of movements and cadence. Cine films were analyzed on a Vanguard Motion Analyzer. The display sites, posturing, and orientation are generally similar in all forms, while the patterns of movement exhibit species and groups differences. These differences were in the height and length of time a pushup was held, repetition of movements, length of pauses between movements and whether the movement involved primarily the front leg actions or actions by both front and hind legs. Display sequences with predictable terminations are Determinate while those which proceed to variable lengths are Indeterminate.

The species-representative display-action-pattern of each species is described in all its characteristics through time and illustrated graphically. No treatment is given to individual or population variations.

Members of the same group generally exhibit similar characteristics in their display-action-patterns, i.e., long or short pushups, hold patterns, volleys, jerkiness, and whether Determinate or Indeterminate. Notable exceptions are *S. jalapae* in the *scalaris* group, *S. nelsoni* in the *pyrocephalus* group, *S. lundelli* in the *spinatus* group, and *S. cryptus* in the *megalepidurus* group. Inter-group similarities can be seen between the *undulatus* and *spinatus* groups, and between the *variabilis*, *chrysostictus* and *merriami* groups.

Sympatric species generally have quite different display-action-patterns, but even within the same group there are some striking similarities, i.e., *S. melanorhinus* and *S. horridus*, *S. cozumelae* and *S. chrysostictus*, and especially *S. graciosus* with *S. undulatus* and *S. occidentalis*. Sympatry with species of other iguanid genera indicates different display-action-patterns.

Smaller species tend to have 4-legged pushups, the larger species front legged pushups. Arboreal forms have slower display sequences while ground and rock dwellers show more rapid and jerky displays. A hypothetical scheme of coordination changes is presented as a speculative way in which such differences in display-action-patterns may have evolved.

### Introduction

The genus *Sceloporus* is the second largest group of lizards in the family Iguanidae and ranges throughout most of North America from New England in the east and British Columbia in the west, south through Mexico to northern Panama in Central America, with the largest number of species concentrated in Mexico. There are 61 species and 126 subspecies recognized as of 1972. These species were divided into 15 species groups by Smith in 1939. More recent work (Larsen and Tanner, 1975) has shown the validity of these groups and there has been little change in their species contents since Smith's original differentiation of them.

The species of *Sceloporus* show a wide diversity in their preferred habitats ranging from deserts and grasslands, tropical forest, deciduous forests, pine forests, cactus and agave forest, and alpine meadows. In these habitats, they are further segregated by their preferences for rock outcrops, sanddunes, beaches, crevices, tree trunks and tree canopies, bunch grass, shrubs, salt flats and gravel plains. They occur from sea level to over 3,000 meters - often two and three species living in close proximity. This diversity provides a great opportunity for the study of the evolution of behavioral patterns.

My interest in the behavior of *Sceloporus* began in the summer of 1955 with a small population of *S. undulatus* along Lake Texoma near the University of Oklahoma Biological Station (Carpenter, 1962). My initial observations on display behavior in wild populations led to the establishment of laboratory populations for controlled observation. Though the consistent pattern of display movements was discerned in *Sceloporus undulatus*, the displays of *Urosaurus ornatus* (Carpenter and Gurbitz, 1961), an iguanid species with a slower display cadence and with a more easily discernible pattern, prompted me to examine the potential for the species-specific nature of the display patterns in iguanid lizards in

general, and in *Sceloporus* in particular. Since 1955, data on the various species of *Sceloporus* (especially behavioral data) have accumulated and form the basis for this report.

This investigation has been supported in part, starting in 1956, by grants from the National Science Foundation (G-2669, G-9062, GB-1972, GB-6517, GB-33986, B16149), the University of Oklahoma Research Institute, the Faculty Research Committee of the University of Oklahoma and the University of Oklahoma Alumni Development Fund. The facilities of the Universities of Oklahoma Department of Zoology and the University of Oklahoma Biological Station are gratefully acknowledged.

Over the years of this investigation, many undergraduate and graduate students have been involved. I wish to acknowledge the following: Marsha Belcher, Louis J. Bussjaeger, Cynthia A. Fite, Ernest A. Gluesing, Susan J. Griffith, William Hayes, Clark McCaskill, Tom McKinney, Dale L. Marcellini, Jeremy E. Penner, James R. Purdue, G.H. Ratzlaff, Billy G. Sanderford, James R. Schwartz, David Taylor, Richard Walker, Sandra Weaver, and Julia K. Yoshida. Appropriate citation of these persons will be made under the species accounts.

### Materials and Methods

The lizards used in this study were obtained by my students and my own field collections and also through trade, gifts, and purchase from other herpetologists and animal dealers. Most were collected on field trips in March and April to the southwestern United States and all of Mexico (except Baja California) over a period of fifteen years. These lizards were carried in the field in especially designed tray cages, which minimized mortality during transport. All lizards were; (1) given an identifying toe clip in the field for each collection stop, and later each individual was additionally toe clipped for individual identification; (2) sexed and measured; (3) given individually identifiable color marks with (DOPE) paint.

All lizards were maintained in cages or indoor and outdoor enclosures at the Animal Behavior Laboratory, University of Oklahoma, Norman, and each summer (June and July) in outdoor enclosures at the University of Oklahoma Biological Station, Lake Texoma near Willis, Oklahoma. Many lizards were held for several months in the cages and enclosures before observations could be made. The lizards were fed an assortment of insects as available; mealworms, crickets, grasshoppers, and other forms collected by sweep net. No particular environmental light or temperature regimes were attempted.

Certain species, especially those of the *torquatus* group, did not perform naturally unless the enclosures were enclosed in a blind. They were observed and photographed through a one-way glass port in a large (5 x 4 x 3 m) environmental chamber, in addition to an outdoor enclosure with a blind.

The enclosures, indoor and outdoor, measured 3.1 x 2.1 x 1 m and 5 x 5 x 1 m with small species in smaller enclosures, the larger species in the larger enclosures. Observations were made between 0900-1100 and 1600 to 1800 hrs.

Early in the investigation extensive notes were recorded by hand and tape recorder, while timings were obtained with a stop watch. Later, cine film became the primary record. Motion pictures were taken from 1959-1964 mainly with a Cine Kocak Species 16 mm movie camera. After 1964, a 16 mm Arriflex with zoom lens was used.

Cine films were initially analyzed by projecting the image onto a screen with gridded numbers and advancing the film frame by frame to record the movements numerically as the image of the displaying lizard moved on the grid. This was satisfactory, but was greatly improved with the acquisition of a Vanguard Motion Analyzer in 1969. The analyzer allows a precise and detailed analysis of cine films with its moveable coordinates provided with a numerical readout. All previous and subsequent films were so analyzed, thus all the data on time-motion of the displays are directly comparable. The numbers obtained from this machine represent the movements of the lizard, through time (its display-action-pattern), and are plotted as the display-action-pattern graph (DAP graph).

Since the motion pictures were taken at varying distances from the performing lizards, with lizards displaying at different angles to the camera, the plotted graphs varied considerably in magnitude, i.e., plotted movements of lizards taken close up appeared more exaggerated than those taken at a distance. However, when considered on the same scale, these differences disappeared. Each plotted graph was studied to recognize time-motion patterns, then by graph squares, the number of squares per movement (unit of movement) and pause between movements, were counted to give the cadence (time) for each unit of movement and pause (interval between units) between units. Each graph square represented a frame(s) from the cine film and the number of frames per second at which the cine film was taken was known.

To establish an objective set of criteria for measuring and comparing aggressive displays, a series of eight categories was devised; site, position, posture, movement types, parts moved, units of movement, sequence, and cadence, and these will be used to assist in describing the aggressive displays of each species of *Sceloporus*

considered. These categories are defined as follows (from Carpenter, 1962a):

*Site* - The place in the habitat (station) from which the lizard performs and the view possible from this station.

*Position* - The orientation of the axes of the lizard with respect to the planes of space, and if pertinent, the intended recipient of the display.

*Posture* - The relative arrangement of the different parts of the body of the lizard.

*Movement type* - The gross relative changes in position and posture.

*Parts moved* - Those parts of the body changing their relationships during the movement of the lizard.

*Units of movement* - A distinct and measurable change in the position and posture, of one or more movement types, which may or may not be repeated.

*Sequence* - The order in appearance of units of movement and the number of units performed in succession.

*Cadence* - The measured time for the performance of each unit of movement and pause between units in a sequence.

The measurements of the last three categories (units of movement, sequence, cadence) provide the time-motion data that describe how the lizard performs his display movements through time. These data then are used as the basis for determining the display-action-pattern (DAP) and can be graphically plotted (DAP graph).

The data for each individual were first compiled and then similarly for each species. The data for each species was then examined and the representative display-action-pattern graph determined from each of the parts of the graph. No determinations of individual variations in display-action-patterns are presented here nor are any statistical manipulations of these data. It is my objective to present what I believe, on the basis of my data, to be the typical or representative display-action-pattern for a particular species from the area(s) I was able to obtain samples, and to give a broad survey of the types of displays for the majority of the species of *Sceloporus*. The comparison of the DAP graphs forms the main basis for this report.

*Taxonomic organization.* The comparative analysis of behavioral patterns is best done under our existing taxonomic framework, therefore I have retained Smith's (1939) formal grouping of species and in no way am I arguing for or against these groups. These subgroups (to be called groups) are: *formosus*, *spinosus*, *undulatus*, *graciosus*, *grammicus*, *megalepidurus*, *torquatus* (Smith's *poinsetti* group), *variabilis*, *merriami*, *maculosus*, *chrysostictus*,

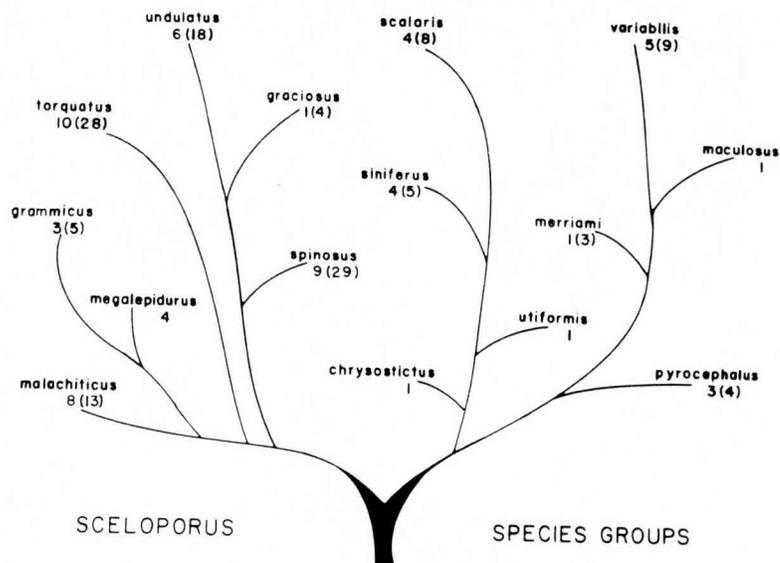


Figure 1. Species groups in the genus *Sceloporus* (after Smith, 1939) indicating proposed phyletic relationships of groups. The number of species and (subspecies) described for each group is given. Outline figures of lizards drawn from motion picture films.

*siniferus*, *utiformis*, *scalaris* and *pyrocephalus*. A phylogenetic tree modified from Smith (1939) indicates his proposed relationships of these groups (Figure 1). This figure also gives the number of species and subspecies (in parenthesis) assigned to each group (these include additional forms described from 1939 to 1972).

In this paper the term "habitat niche" is used to differentiate between the broad general term habitat and the very specific term ecological niche, with respect to habitat preference or partitioning. The habitat niche refers to the substrate occupied by a species, such as, rocky outcrops, boulders, logs, tree trunks, fence posts, ground, grass clumps, etc.

#### Behavioral Repertoire of *Sceloporus*

Agonistic behaviors (including aggression, dominance, submission, and female rejection to courtship), courtship and copulation I believe to be stereotypic.

Only stereotypic aggressive displays of *Sceloporus* will be discussed herein. I strongly believe that through the study of stereotypic behavior we will be able to gain further knowledge on the relationships of populations and the higher taxonomic categories. Similarly the interpopulation variation of stereotypic behavioral

patterns may enable a better understanding of the evolution of behavioral patterns.

Aggressive behavior appears in all species of *Sceloporus*. Aggression is also characteristic of all of the iguanid lizards so far observed (Carpenter, 1967). Aggressive actions include displays, attacks, fighting, biting and chasing. Aggression usually establishes dominance and subordination, which may vary in degree and has been observed in all groups of *Sceloporus*. In natural populations such dominance is related to territoriality, whereas in laboratory populations it may appear as despotism where one male dominates all others, or a co-dominance may be present (Carpenter, 1961). Shifts in dominance can easily be effected by removal of the dominant or despot; a new dominant then arises from the remaining males (Carpenter, 1967).

The aggressive displays of *Sceloporus* show different behavioral patterns among the numerous species, therefore they are considered to be species-specific (species-typical, species-characteristic), though subspecific and population variations, as well as slight individual variation, are to be expected. Evidence indicating that these different aggressive displays are genetically determined comes from 1) the consistent pattern of the display-action-pattern within a species; 2) the appearance of the display-action-pattern in newly hatched or newly born individuals, often within minutes of taking their first breath (Carpenter, 1960); 3) the appearance of the species-specific display in isolation (Yoshida, 1966); 4) the absence of display alteration when associated with other species through time or by captivity; 5) the similarity of displays of closely related forms; 6) the presence of genetic intermediates [not shown in *Sceloporus*, but in *Anolis* (Gorman, 1969)].

The aggressive displays of *Sceloporus* are associated with territoriality in natural populations and dominance in laboratory populations. Thus, it is an important determinant of social structure (Carpenter, 1967).

No significant differences have been observed in the manner in which the males attack, bite, fight, and chase conspecific males. Though not recorded for all of the species considered herein, the consistency in related behaviors (displays and courtship) strongly suggest that all *Sceloporus* will possess a similar aggressive behavioral pattern, and deviations result from ecological niche differences.

Attack behavior, fighting, biting, and chasing as well as dominance relationships are closely allied with the aggressive display

of each species. Since the aggressive displays show species - specific patterns, they shall be considered separately and mentioned in the context of the other aggressive behaviors only as aggressive displays.

When a male challenges another by an aggressive display and neither one retreats, they may lunge toward one another and attempt to bite the adversary. If a bite hold is obtained by one or both, the two males may roll over and over until the holds are broken. This fighting behavior may also take the form of tail fighting or tail lashing; each male swings his tail at the head of his adversary as they align laterally head to tail at close range. A male may rush at another male and bite his tail, a leg, some region of his body or head; leg or tail is most likely. Fights may last but a second or two or continue off and on for over an hour, the males resting then continuing their attacks until one ultimately retreats with the winner usually chasing the retreating male; this pursuit may be only a few centimeters or a few meters.

Once dominance is established, subordinate males often exhibit a characteristic submissive posture (Fig. 2b, 2c) by flattening the body and head and tail against the substrate, with the legs spread, and the eyes often closed. The submissive posture usually stops the aggressive actions of the dominant male. Were the subordinate male to move from his submissive posture, he may immediately be attacked by the dominant if the latter is still near. Females exhibit a rejection posture (Carpenter, 1962a) which also appears to stop aggressive actions by males (Fig. 2d).

#### *Display-Action-Patterns (DAP)*

For the comparison of behavioral patterns in *Sceloporus*, I use the aggressive displays with particular emphasis on the display-action-patterns. The display action-pattern includes all the behavioral actions associated with the establishment and maintenance of reproductive isolation and success.

Though the site and position (orientation) are not involved in the time-motion events of the display-action-pattern, they are important parts of the total display in the ecological and visual presentation contexts.

Site. — Most species of *Sceloporus* display from raised areas in the habitat; and those that do not, or also display frequently at other sites, will be mentioned specifically under species descriptions.

Orientation. — The orientation assumed during a display by a male *Sceloporus* is related to the intensity of the display (assertion, challenge, see below) and the habitat. Arboreal species may display with the body in a vertical, horizontal, or various oblique positions, heading either up or down.

Posture. — Posture relates to the arrangement of the various body parts and variations in posture, or elaboration in posturing generally related to the intensity of the display. The dewlap (throat expansion) of some species appears to be proportionately greater than in others. Some species appear to have a greater lateral compression of the trunk.

Assertion Display. — During assertion display, the performing lizard produces very little posturing, the movements are usually of lower amplitude (height) and the lizard does not orient in any particular direction. The context within which the assertion display is performed is variable, but is characteristically performed when a lizard stops as it moves about in its habitat, as if to declare its presence to other lizards which might be in view.

Challenge Display. — The high intensity challenge display occurs with the lizard oriented in a particular direction and effecting specific postural changes (Fig. 2a, 2b, 2c, 3a, 3b, 3c, 3d). The amplitude of the display movements is maximum.

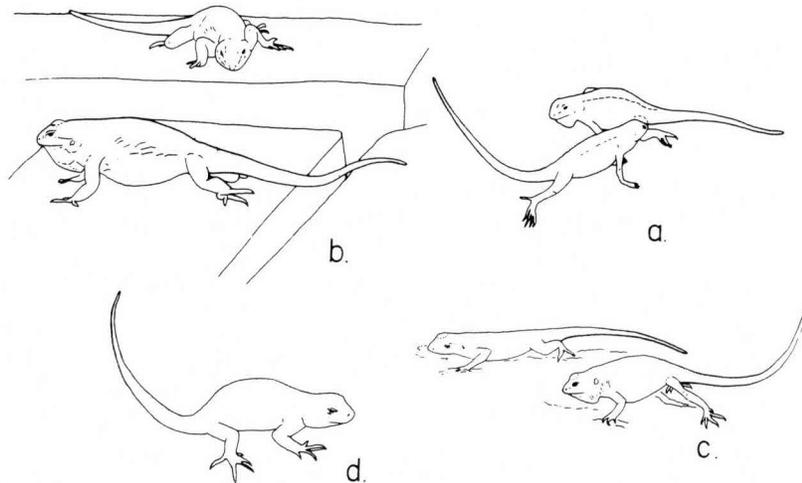


Figure 2. a - Face-off orientation between two challenging males (*S. siniferus*), characterized by challenge posture, lateral presentation at close range, the two individuals heading in opposite directions, with forelegs extended; b - Submissive posture of male to challenging male, submission characterized by the submitting lizard flattening on the substrate, legs spread, head down, eyes partly or completely closed (*S. clarki*); c - Same posture seen in b (*S. utiformis*); d - Rejection posture by female (*S. undulatus*), characterized by arching back, crouching with head lowered, inflating trunk region and raising (often waving) of the tail.

The typical position or orientation of a male *Sceloporus* during a challenge display is broadside (lateral presentation), i.e., per-

pendicular to the object being challenged (almost always a conspecific lizard). At close range (5-10 cm), two males challenging lie parallel usually facing opposite directions. This particular close range orientation is called the face off (Fig. 2a, 2c). Lateral presentation, at either close range or a distance, can be emphasized by tilting the long axis of the body towards the adversary, i.e., if the adversary were above him, he would tilt or tip his long axis upward.

The typical posture of challenging *Sceloporus* includes marked changes in body proportions and shape of throat, the trunk, and the legs (Fig. 2a, 2b, 2c, 3a, 3b, 3c, 3d). The throat (or gular) region expands ventrally (as a dewlap) and increases the laterally viewed size and shape of the head and neck region. The throat remains expanded for the duration of a display and is not pulsed out and back. The back is arched dorsally to varying degrees, depending on the species and the intensity of the display, while the entire trunk region is compressed (particularly ventrally) laterally through increasing the dorso-ventral diameter of the trunk. Depending on the species, the lizard may rise on just the front legs, or all four legs (4-leg rise). The head is usually parallel to the trunk or slightly lowered.

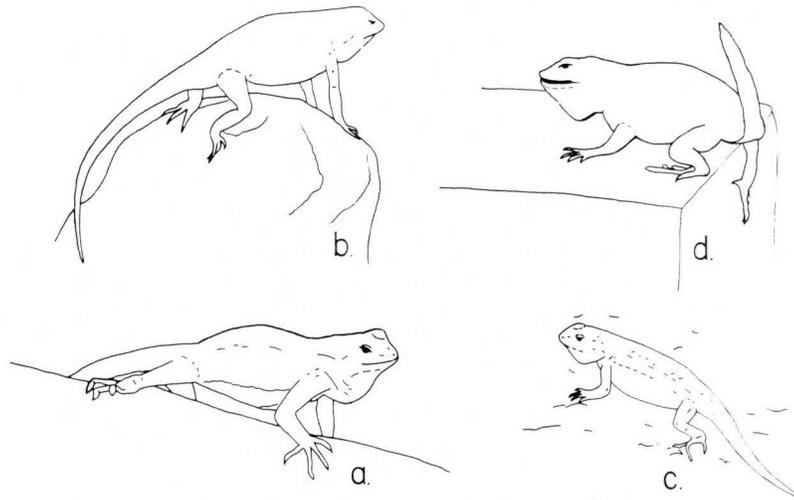


Figure 3. Postures assumed during challenge displays of male in four species of *Sceloporus* (belonging to four different groups), characterized by slight arching of the back, lateral compression of the trunk exposing the abdomen, extension of the dewlap, often accompanied by movements of the tail: a - *S. grammicus*; b - *S. teapensis*; c - *S. jalapae*; d - *S. jarrovi*.

These postural and body shape changes dramatically increase the laterally viewed size of the challenging lizard and expose the special color patches on the males of most species. These color patches are usually located in the throat midline and the ventral and ventro-lateral aspects of the trunk. These patches are generally present (with exceptions) as sexually dimorphic characters on male *Sceloporus*.

Assertion and challenge are considered as only difference in intensity of the display and gradations in intensity between these two extremes are frequent.

The ventral coloration is often visible anteriorly when a male is in an alert posture on a raised lookout. The ventral color or color pattern, visible in the alert posture, may be important in other social contexts, but remain to be confirmed.

To quantify postural change, Purdue and Carpenter (1968) measured *S. teapensis*. Cine images of a male perpendicular to the camera lens were projected onto a grid and traced. By determining the increase in surface area of the same individual in a challenge posture in contrast to an alert posture, the percentage of area change was derived. The head and expanded throat increase the presentation area by 15 percent. The laterally compressed trunk increases presentation area by 13 percent. Males of *S. teapensis* have ventral and lateral bright longitudinal color patches on the trunk (blue ventrally, pink (lavender) ventrolaterally, and yellow laterally). Lateral compression brings the ventral color into view, increases the visible area of pink, and slightly increases the yellow area - 100, 49 and 3 percent, respectively. Though the increase in trunk area is slight, the increase in exposure of the bright colors is great.

**Body Movements.** — All *Sceloporus* display certain pushup movements of the body through the extension and flexion of the legs. Different pushup patterns occur in different species. Some do only front leg pushups, others four leg pushups or some intermediate pushups (Purdue and Carpenter, 1972a). Some species include a vertical up and down motion of the head (head bobs).

The effect of these pushup and bobbing actions is to move the head alone (rare in *Sceloporus*, except at very low intensities), the head, neck and anterior trunk region (2-legged pushup), or the entire body of the lizard in varying degrees (4-legged pushup).

Some species add tail twitching or tail waving, but this is usually not directly related to the display (in some iguanid genera, tail action may be a part of the display).

**Rhythm of movement.** — The actions of the various body movements, in particular the pushups, move the animal up and down and are related to the sequential duration of the components of

the display. The length of time a lizard holds each display posture is arbitrarily divided into a long unit (0.50 sec or longer) and a short unit (less than 0.5 sec).

The term *unit* as used in the descriptions of the display-action-patterns was arbitrarily selected to describe a portion or segment of the total time-motion events of the display which could be recognized, timed, and used for comparison. A unit, thus, is a measurement of the pattern of raising and lowering of the lizard, whether this action is of long or short duration, rises to full height (fully extended legs) or some approximate fraction of full height, how the movement holds at certain heights, etc. The term unit is best understood by examining the DAP graph of a species while reading the description of the body movements for this species.

**Amplitude** (height) varies from high with legs fully extended (sometimes up on the outer digits of the toes) to **medium** height with the legs only partially extended, to **low** with the legs flexed to bring the body only slightly off of the substrate. These may vary with the intensity of the display, but usually in the consistent display pattern, i.e., if the high amplitude unit is performed lower, the low amplitude unit is also relatively lower. A **dip** is the performance of a quick movement from a high or medium amplitude to a very low amplitude and back to a higher amplitude. Arrangement of units - units may be performed in **rapid** succession, they may be **spread out** with the long pauses in between, or they may be **grouped** in volleys, with pauses between volleys. Grouped volleys may consist of two units (doublets), three units (triplets), etc. The beginning unit(s) (initial) may differ from succeeding units, and **terminal units** may also differ from preceding, more consistent, units. A unit that is consistent, frequent and repeated is referred to as the **basic unit** within a display. Units of different types may **alternate** in their appearance.

The order in which the units appear in a display performance is the **sequence** and with the temporal relationships, forms the display-action-pattern. These will be considered below for each species. Sequences have certain characteristics separate from the units which form them. **Determinate sequence** - the order of appearance of the units and pauses forming the sequences are usually predictable and are repeated after a pause. **Indeterminate sequence** - in contrast to the determinate sequence, the number of units which appear in succession is variable, with the performer starting his display and producing variable numbers of units in succession before stopping. The lizard usually does not display again except after a long pause. Relatively, some sequences are long (5 sec or more) while others may be short (less than one sec). **Acceleration and deceleration** - the cadence is usually quite

consistent, but the speed of the performance of a display-action-pattern (cadence) is an important characteristic, for some perform rapidly, others slowly, thus producing a fast or slow cadence, of both units and/or the entire sequence. The cadence is affected by the length of time for the pauses between units and between sequences. Sequences may be repeated a number of times with short or long pauses in between.

Rapid pushups, or pushups with quick changes in amplitude produce a movement which appears jerky. A lizard rising or lowering rapidly and then stopping, especially the latter, will produce a very short jerky movement which is seen in many displays.

When the information on the sequence of the units of movement through time was obtained, for each species, it was plotted graphically producing a representative display-action-pattern graph (DAP graph) for each species. To illustrate the sequence of movements through time an outline figure of a displaying male *S. teapensis* performing pushups is presented in Figure 4 and is synchronized with its representative display-action-pattern graph.

#### Synopsis of *Sceloporus* Behavior

The following data synopsis includes descriptions of a representative display-action-pattern (DAP), the social and ecological aspects related to DAPs for 42 species of *Sceloporus*.

The sample size for each species was quite variable. The sample sizes for construction of the DAP are listed in Table 1. Many more displays were observed, along with other behaviors, than could be economically and efficiently studied. The consistency of behavioral patterns in those species represented by large samples, I believe, supports the reliability of the DAPs constructed from smaller samples, at least for the population at the sample localities.

Table 1. The sample sized used to determine the display-action-patterns of *Sceloporus* used: number of cine sequences, individuals, and collecting sites, respectively.

Species	Sequences	Individuals	Localities Collected
formosus	84	5	1
acanthinus	7	3	1
asper	25	3	3
lunaei	59	8	3
ornatus	56	6	2
dugesii	116	10	2
jarrovi	33	1	1
mucronatus	24	3	1
poinsetti	60	6	3
torquatus	44	4	2
cryptus	40	2	1

megalepidurus	28	1	1
grammicus	82	10	6
graciosus*	10	2	2
cautus	18	2	2
woodi	4	2	1
occidentalis	21	3	3
undulatus	113	5	3
lundelli	4	1	1
edwardtaylori	42	9	2
melanorhinus	151	14	5
clarki	59	13	3
orcutti	78	14	2
magister	47	10	3
horridus	245	32	16
olivaceus	48	4	3
spinosus	144	21	11
pyrocephalus	52	6	4
nelsoni	51	7	3
merriami	30	5	2
maculosus	24	2	2
parvus	60	5	2
couchi	46	4	1
cozulemae	25	1	1
teapensis	75	14	5
variabilis	86	9	7
chrysostictus	54	5	1
siniferus	104	13	3
utiformis	43	1	1
aeneus	16	7	2
scalaris	76	10	3
jalapae	101	8	3
	2485	291	124

\*Data also provided by G.W. Ferguson

The ratio included in some body movements sections indicates the relative movements of the fore legs (measured in shoulder region) to the hind legs (measured in hip region) during a comparable pushup cycle. The vertical distance from the low to the high point of shoulder (S) or hip (H) movements was measured (Purdue and Carpenter, 1972a). S larger than H indicates more movement of the anterior body, i.e., primarily a front-legged pushup, whereas S nearly equal to H indicates a four-legged pushup.

The description of the display-action-pattern should be used to examine the display-action-pattern graph for each species

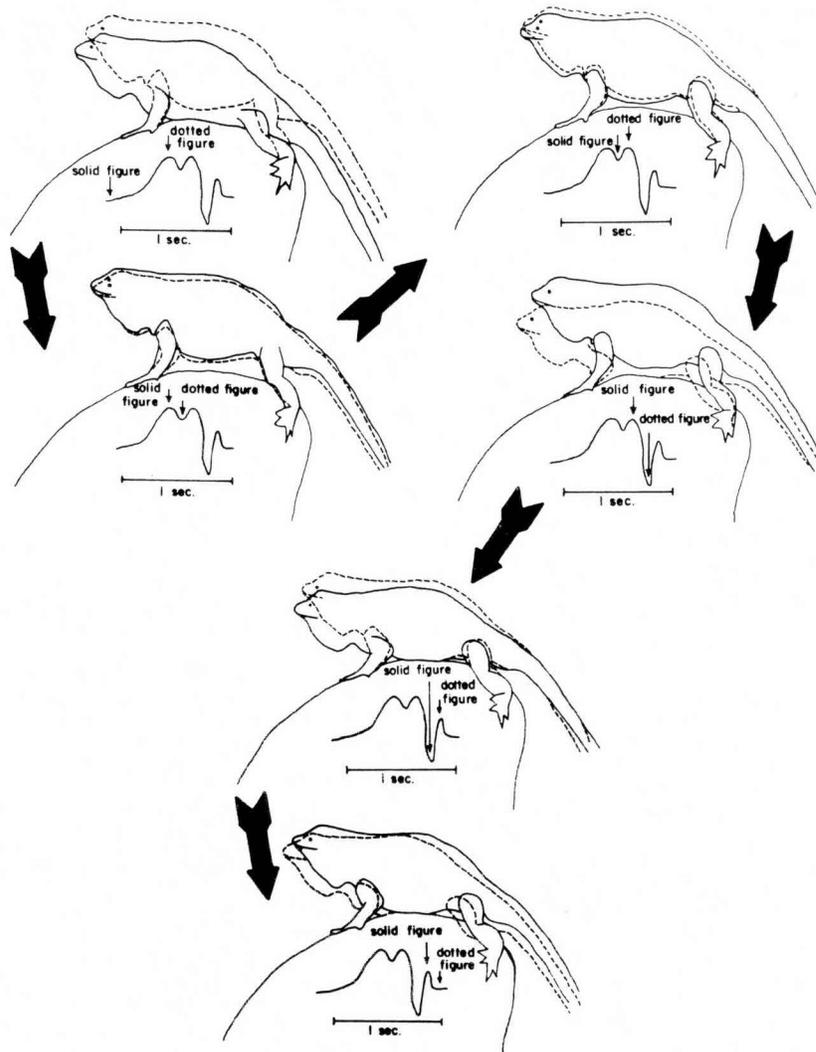


Figure 4. A series of sketches demonstrating the time-motion events during the performance of a challenge display and depicting a synchronized display-action-pattern graph (*S. teapensis*).

(See figures) and indicates the type of movements, units of movement (U), sequences (S), pauses, and cadence of units, sequences, and pauses. Unless otherwise indicated, the display-action-patterns are for males.

### Formosus Group

#### *Sceloporus formosus*

**Habitat** — arboreal, forest dwellers at high altitudes, log piles.

**Social system** — territorial (field), despotism or dominance in enclosures.

#### DAP (Figure 5)

Site: raised area.

Orientation: lateral presentation, tilting.

Posture: exhibits, dewlap, lateral compression, arches back, rises on all four legs.

Body movements: movements in head, neck and anterior trunk by 2-legged pushups with flexion and extension of front legs, very little action in hind legs.

Sequence: Indeterminate.

Description: A series of three or more units. First unit - rapid rise to full height with a jerky stop, hold, then lower to low amplitude (1.31 sec.), pause (0.69); 2nd unit - rapid rise to full height with a jerky stop, hold, and down to low amplitude (1.25), pause (0.19); 3rd unit - rapid rise to full height, short hold, down to medium height, hold, then down to low amplitude (1.38), pause (0.13); 4th unit - rise almost to full height followed immediately by slight lowering, hold, and then down (1.06), no pause, but immediate rise and repeating of 4th unit, these repetitions continuing jerkily with lower amplitudes in height and not going down as low and with no pauses between units; 5th (0.81), 6th (0.81), 7th (0.81), the number of successive units variable.

The 3rd unit is different from the others in that it is held at high amplitude and then at medium amplitude before lowering. It is then followed by a more rapid cadence.

Sample: 84 sequences, 5 individuals, 1 locality.

Collection site: Llano de los Flores, 17-25 km north of Ixtlan, Oaxaca, Mexico, March 25, 1970.

Sympatry: *Sceloporus* - *aeneus*, *cryptus*, *grammicus*.

References: Bussjaeger, 1971.

#### *Sceloporus asper*

**Habitat**: arboreal, open oak woodland in mountains.

**Social system**: unknown.

DAP (Figure 5)

Site: raised area.

Orientation: lateral presentation and face off, tilt, may display vertically, but usually horizontally.

Posture: lateral compression, dewlap.

Body movements: movements in head, neck and anterior trunk by 2-legged pushups with extension and flexion of the front legs.

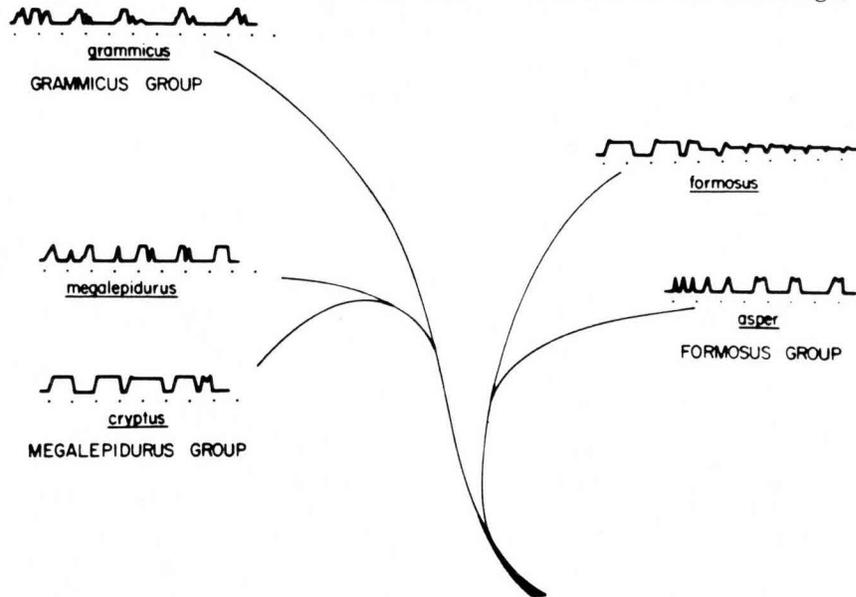


Figure 5. Display-action-pattern graphs for species members of the *formosus*, *megalepidurus* and *grammicus* groups of *Sceloporus*. Dots below graphs indicate one second intervals in time.

Sequence: Indeterminate.

Description: A series of pushups of increasing length, the first three very rapid. 1st unit - rapid rise to full height and immediate return to low amplitude (0.13 sec), pause (0.13), 2nd Unit (0.25), pause (0.19), 3rd Unit (0.19), pause (0.38), 4th Unit (0.31), pause (0.90), 5th Unit (0.38), pause (0.88), 6th Unit - rapid rise to full height with jerky stop, slight rise again and down to low amplitude (0.63), pause (0.88), 7th and 8th similar to 6th, (0.56), pause (1.13), 8th (0.63).

The features to be noted are the rapid beginning with decreasing tempo, the length of the pushups and pauses increasing.

Sample: 25 sequences, 3 individuals, 3 localities (within 19 km of each other).

Collection site: 17 to 36 km E of Tepic (near Highway 15),  
Nayarit, Mexico. May 7, 1968.  
Sympatry: Unknown  
Reference: Bussjaeger, 1971.

#### Megalepidurus Group

##### *Sceloporus megalepidurus*

**Habitat:** associated with agave clumps on barren hillside with some sparse vegetation.

**Social system:** unknown.

##### DAP (Figure 5)

Site: raised areas near ground, or on ground.

Orientation: unknown, challenge display not observed.

Posture: dewlap, some lateral compression.

Body movements: movements in the head, neck and trunk by 2-legged pushups with flexion and extension of the front legs, or with some, but much less, action in hind legs.

Sequence: Indeterminate.

Description: A series of irregular pushups. U1 - rise to full height and immediate lowering to low amplitude (0.56 sec), pause (0.44), U2 - rapid pushup to 2/3 full height and down (0.25), pause (0.31), U3 - rise, with jerk to full height, short hold, and down (0.56), pause (0.88), U4 - rapid full height pushup, down (0.25), pause (0.63), U5 + U6 - full height pushup with hold, down, immediately rising to almost full height and down with hold (double) (0.81), pause, (0.94), U7 + U8 - (same as U5 + U6) (0.63), pause (0.94), U9 - full height pushup with hold and down (0.69).

Note initial units are rapid, and units 5 through 8 form two doubles.

Sample: 28 sequences, 1 individual, 1 locality.

Collection site: 18 km S. of Acultzingo, Puebla, Mexico. March 24, 1970.

Sympatry: *Sceloporus grammicus*.

##### *Sceloporus cryptus*

**Habitat:** Pine forest dwellers at high altitudes. Logs and log piles, tree trunks.

**Social system:** unknown.

##### DAP (Figure 5)

Site: raised area.

Orientation: lateral presentation.

Posture: lateral compression, dewlap.

Body movements: Movements in head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.

Sequence: Indeterminate

Description: A series of long pushups. U1 - rise to full height, long hold, and down to low amplitude (1.13 sec), pause (0.81), U2 - similar pushup (1.19), pause (0.19), U3 - rise to full height with jerky stop at top, long hold, down to low amplitude (1.63), pause (0.38) U4 - full height pushup with hold (1.0), pause (0.13), U5 - rise to full height with jerky hold, down to low amplitude (0.56).

Note that U3 pushup is held at full height longer, after a short pause between U2 and U3.

Sample: 40 sequences, 2 individuals, 1 locality.

Collection Site: Llano de los Flores, Sierra de Juarez, Distrito Ixtlan, Oaxaca, Mexico. March 25, 1970.

Sympatry: *Sceloporus - aeneus, formosus, grammicus*.

#### Grammicus Group

##### *Sceloporus grammicus*

Habitat: Open areas at high altitudes and in pine forests. Logs and log piles.

Social system: territorial, dominance and despotism in enclosures, male with harem of females.

##### DAP (Fig. 5)

Site: raised area and on ground.

Orientation: lateral presentation and face off, from horizontal or vertical surfaces.

Posture: lateral compression, dewlap.

Body movements: movements in the head, neck and trunk by 2-legged pushups with extension and flexion of front legs; some, but much less, action in the hind legs. Ratio S = 0.717 H = 0.599.

Description: A series of repeated rapid sequences. S1 - rapid rise with jerk to full height and down, short pause, rapid rise to full height, short hold, down, back up immediately, short hold, and down (1.56 sec), pause (0.75), S2 - rapid rise with jerk to full height, short hold, down, quickly up to 2/3 height, down, jerk up and down to 1/2 amplitude, short hold, down quickly, up to 1/2 height, down, up to 1/4 height and down (1.31), pause (1.25), S4 - rapid rise with jerk to full height, short hold, down, quickly up to 1/2 height, down (0.88), pause (1.25), S5 - similar to S4 (0.88).

Initial sequence has three units, which appear to be repeated in succeeding sequences with greater emphasis on first unit.

Sample: 82 sequences, 10 individuals, 6 localities.

Collection sites: (1) La Joya, Veracruz, Mexico. Mar. 23, 1970;

(2) Ruins of Cholula, Puebla, Mexico. Mar. 29, 1966; (3) 13 km NW of Actopan, Hidalgo, Mexico. Mar. 30, 1966; (4) Jicquipilco, 40 km N of Toluca, Mexico. Dec. 16, 1964; (5) Mt. Popocatepetl, Mexico. June 1961; (6) 19 km N of Ixtlan, Oaxaca, Mexico. Mar. 25, 1970; (7) 6 km SW of Buenos Aires, Hw 40, Durango, Mexico. Mar. 23, 1971.

Sympatry: *Sceloporus* - *aeneus*, *cryptus*, *formosus*, *jarrovi*, *megalepidurus*, *poinsetti*.

References: Axrell and Axtell, 1970; Carpenter, 1961; Evans, 1946; Evans 1953; Evans, 1955; Fite and Carpenter, 1970; Gluesing and Carpenter, 1971; McKinney and Carpenter, 1966; Milstead, 1970; Muliak, 1936; Purdue and Carpenter, 1972a, 1972b; Smith, 1946; Yoshida, 1966.

### Torquatus Group

#### *Sceloporus ornatus*

**Habitat:** desert, rocky outcrops of low desert hills; crevice dweller.  
**Social system:** dominance in enclosure; semi gregarious.

#### DAP (Fig. 6)

Site: raised area.

Orientation: lateral presentation and face off.

Posture: lateral compression, dewlap.

Body movements: movements of head, neck and anterior trunk by 2-legged pushup with extension and flexion of front legs.

Sequence: Indeterminate.

Description: A series of irregular, jerky, pushups, with suggested pattern. U1 - rise to full height and immediately down to 1/4 amplitude, (0.56), pause, (0.19), U2 - rapid rise to 2/3 height and down, (0.19), U3 - rise to 2/3 height and down (1.19), pause (0.31), U4 - rise to 1/4 height, jerk, up to 2/3 height, jerk, to full height, short hold, down to low amplitude (1.0), pause (1.31), U5 - rise to full height and down (0.38), pause (0.44), U6 - rise to 3/4 height and down to 1/4 amplitude (0.25), pause (0.13), U7 - rise to 1/2 height, jerk, up to 2/3 height, jerk, to full height, hold, down (1.13).

Note that there appears to be a repeated sequence U1 through U4 and U5 through U7, with only a slight variation, i.e., U2 and U3 forming a double pushup, U6 a single pushup.

Sample: 56 sequences, 6 individuals, 2 localities.

Collections sites: (1) 96 km W of Saltillo, Coahuila, Mexico along Highway 40. Mar. 31, 1969; (2) 53 km E of San Pedro de las Colonias, Coahuila, Mexico along Highway 40. May 31, 1969.

References: Hunsaker, 1962; Purdue and Carpenter, 1972b.

### **Sceloporus dugesii**

**Habitat:** rock walls, rocky outcrops, boulders with crevices, open or shrubby vegetation.

**Social system:** gregarious (especially females), territorial, dominance in enclosures.

#### **DAP (Fig. 6)**

Site: raised area on rock surfaces.

Orientation: lateral presentation and face off, tilt.

Posture: lateral compression, dewlap, arch back, rise on four legs.

Body movements: movements of head, neck and trunk by 2-legged pushup with extension and flexion of front legs; may be preceded by a jerky bounce.

Sequence: Determinate.

Description: A series of repeated jerky sequences. S1 - rapid rise to full height, deep jerk, down to 1/2 amplitude, short hold, down to low amplitude, short hold, a series of four decreasing jerks, (1.06), pause, (0.94), S2 through S4 similar with only two jerks each at the end of each sequence, S2 - (1.19), pause (1.0), S3 - (1.19), pause (0.88), S4 - (1.13).

Note that the pattern is a rapid jerky sequence which is repeated.

Sample: 116 sequences, 10 individuals, 2 localities.

Collection sites: (1) 64 km S of Guadalajara, Jalisco, Mexico, Mar. 27, 1967. (2) Lago Cuitzeo causeway, 30 km N of Morelia, Michoacan, Mexico, Mar. 30, 1967.

Sympatry: *Sceloporus - horridus, parvus, scalaris, torquatus*.

References: Hunsaker, 1962; Purdue and Carpenter, 1972a, 1972b, Schwartz and Carpenter, 1969; Walker and Carpenter, 1967.

### **Sceloporus jarrovi**

**Habitat:** rocky outcrops with crevices, rocky walls, rocky slopes, open areas, open forests with large boulders.

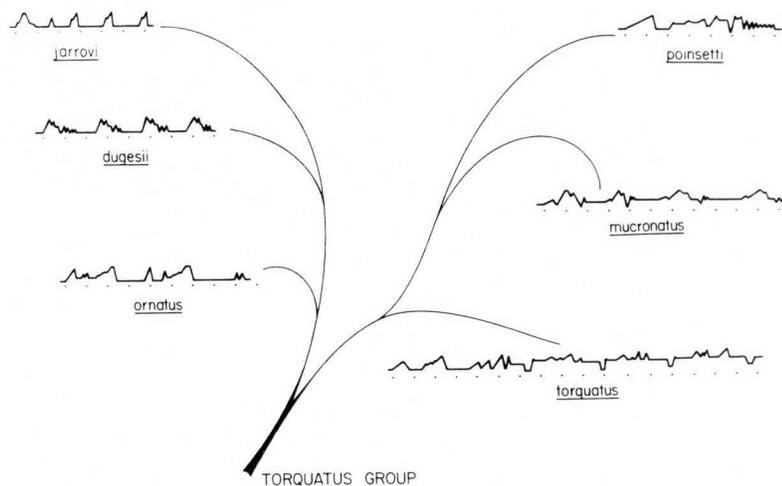


Figure 6. Display-action-pattern graphs of species members of the *torquatus* groups of *Sceloporus*. Dots below graphs indicate one second intervals in time.

Social system: territorial; dominance in enclosures.

DAP (Fig. 6)

Site: raised area.

Orientation: lateral presentation, face off.

Posture: lateral compression, dewlap.

Body movements: movements of head, neck and anterior trunk by 2-legged pushup with extension and flexion of front legs.

Sequence: Indeterminate.

Description: A series of repeated similar pushups after a differing initial pushups. U1 - rise to 1/3 height, jerk, up to full height, short hold, down to 1/4 amplitude, jerk hold, down to low amplitude (0.94), pause (0.63), U2 - rise to 2/3 height and down (0.25), U3 - rise to 1/2 height, jerk to full height and down, (0.38), pause (1.19), U4 - and U5 similar to U3, U4 (0.44), pause (1.12), U5 (0.38).

Note that after the initial first two units, the remaining units are repeated, at a rapid cadence.

Sample: 33 sequences, 1 individual, 1 locality.

Collection site: 11 km W of Portale, Cochise Co., Arizona. Apr. 3, 1969.

Sympatry: *Sceloporus* - *grammicus*, *mucronatus*, *poinsetti*, *scalaris*, *virgatus*.

References: Axtell and Axtell, 1971; Carpenter, 1960; Gloyd, 1937; Himstedt, 1969; Hunsaker, 1962; Smith, 1946.

### **Sceloporus mucronatus**

**Habitat:** rocky outcrops and boulders with crevices in open areas, open forests.

**Social system:** gregarious, territorial, dominance and despotism in enclosures.

**DAP (Fig. 6)**

Site: raised area on rock surface.

Orientation: lateral presentation, face off, horizontal or vertical.

Posture: lateral compression (not pronounced), dewlap.

Body movements: movements of head, neck and anterior trunk by 2-legged pushup with extension and flexion of front legs. Ratio;  $S = 0.732$   $H = 0.097$ .

Sequence: Determinate.

Description: A series of jerky sequences with repeated pattern. S1 - rise to 1/4 height and down, short hold, rise to full height with short hold, down to 3/4 amplitude, jerk up and down to very low amplitude (deep dip) back up to 1/4 height with jerk (1.94), pause (0.94), S2 - through S4 similar to S1, S2 (1.44, pause (1.13), S3 (2.25), pause (1.63), S4 (2.0).

Note that a series of repeated and jerky sequences varying in cadence. Note the presence of a deep dip near end of each sequence.

Sample: 24 sequences, 3 individuals, 1 locality.

Collection site: La Joya, 24 km NW of Jalapa, Veracruz, Mexico. Mar. 28, 1966.

Sympatry: *Sceloporus - jalapae, jarrovi, spinosus, torquatus*.

References: Hunsaker, 1962; Purdue and Carpenter, 1972a, 1972b; Walker and Carpenter, 1967.

### **Sceloporus poinsetti**

**Habitat:** rocky outcrops and boulders, desert and forested areas, crevice dweller.

**Social system:** possibly gregarious, territorial in nature, dominance and despotism in enclosures.

**DAP (Fig. 6)**

Site: raised areas, particularly rocky surfaces near crevices.

Orientation: lateral presentation, face off.

Posture: lateral compression, bloating, dewlap.

Body movements: movements of head, neck and anterior trunk by 2-legged pushup with extension and flexion of front legs. Ratio:  $S = 0.807$   $H = 0.206$ .

Sequence: Determinate.

Description: A very long, jerky, unrepeated sequence with a very jerky ending. U1 - slow rise to full height and quickly down to low amplitude (1.38), pause (0.56), U2 - rise to 1/2 height with

jerk stop, hold, (0.69), U3 - slight rise with jerk, hold and rise to 3/4 height and down (0.75), pause (0.13), U4 - rise to full height and down to 3/4 amplitude, hold, down to very low amplitude (deep dip) (0.94), pause (0.06), rise to full height with jerk hold, down to low amplitude (0.56), no pause but a series of rapid jerky pushups starting up to 3/4 height and descending, U6 - (0.25), U7 - (0.19), U8 - (0.19), U9 (0.25), U10 - (0.19).

Note that this is a long sequence with no repeated pattern and with a deep dip between U4 and U5, and with rapid jerks terminating the sequence.

Sample: 60 sequences, 6 individuals, 3 localities.

Collection sites: (1) 142 km W of Durango, Durango, Mexico. Mar. 20, 1965; (2) 65 km S of Monclova, Highway 57, Coahuila, Mexico. Mar. 29, 1969; (3) 19 km N of Pedricena, Durango, Mexico. April 1, 1969.

Sympatry: *Sceloporus - aeneus, grammicus, jarrovi, maculosus, parvus, scalaris.*

References: Hunsaker, 1962; Purdue and Carpenter, 1972a, 1972b, Pyburn, 1955; Schwartz and Carpenter, 1969; Weaver and Carpenter, 1969.

#### **Sceloporus torquatus**

**Habitat:** boulders with crevices, rocky outcrops with crevices; open fields and forest openings.

**Social System:** territorial; dominance and despotism in enclosures. DAP (Fig. 6)

Site: raised area on rocky surfaces.

Orientation: lateral presentation, face off.

Posture: lateral compression, bloat, dewlap, arch back.

Body movements: movements of head, neck and anterior trunk by 2-legged pushup with extension and flexion of front legs.

Radio: S = 0.694 H = 0.155

Sequence: Determinate.

Description: A series of apparently repeated sequences after two different initial units. Prolonged and jerky. U1 - rise to 2/3 height and down (0.81), pause (0.56), U2 - slow rise with three jerks to full height, and down (1.19), pause (1.06), S1 (following units 1 and 2), rise to 1/2 height and down, short hold, rise to 3/4 height and jerk down to 1/2 amplitude, long hold, rapidly down to very low amplitude, (2.63), pause (0.25), S2 - rapid rise to 2/3 height with jerk stop, hold, up to 3/4 height, down, jerk, up to full height, down to 1/2 amplitude, short hold, jerk up and back to 1/2 amplitude, long hold, rapid drop to low amplitude (deep dip) (3.31), pause (0.19), S3 and S4 similar to S2, S3 - (1.13), pause (0.19), S4 - (3.50).

Note that the first two units differ from the apparently repeat-

ed sequences that follow S1 through S4. In the long sequences, which are held at medium or higher height, the end of each has a deep dip to low amplitude.

Sample: 44 sequences, 4 individuals, 3 localities.

Collection sites: (1) 13 km S of Mexico City, Mexico, Mexico. Mar. 22, 1968; (2) Lago Cuitzeo, Michoacan, Mexico. Mar. 31, 1966; (3) 16 km S of Mexico City, Morelos, Mexico. Aug. 16, 1967.

Sympatry: *Sceloporus - dugesii, jalapae, mucronatus, spinosus*.

References: Hunsaker, 1962; Purdue and Carpenter, 1972a, 1972b; Schwartz and Carpenter, 1969; Walker and Carpenter, 1967.

### Graciosus Group

#### *Sceloporus graciosus*

**Habitat:** open forest, sagebrush flats, scrubby hillsides to high elevations; terrestrial, but will climb.

**Social system:** territorial in nature, dominance and despotism in enclosures.

DAP (Fig. 7)

Site: raised area.

Orientation: lateral presentation, face off.

Posture: lateral compression, dewlap

Body movements: movements of head, neck and anterior trunk, often with rise on all four legs, by 2-legged pushup with extension and flexion of front legs.

Sequence: Indeterminate.

Description: A series of three initial units followed by a series of doublets. U1 - rise to full height, hold, down, (0.62), pause (0.88), U2-rise to full height, short hold, down (0.25), pause (0.88), U3 - rise to full height, hold, down (0.44), pause (0.81), U4 + U5 (doublet) rise to 3/4 height, short hold, down to 1/4 amplitude, short hold, rise to full height, hold, down (0.88), pause (0.94), U6 + U7 and U8 + U9 (similar to doublets U4 and U5), U6 + U7 (0.94), pause (0.88), U8 + U9 (1.00).

Note that after the initial three units, a pattern of doublets follows.

Sample: 10 sequences, 2 individuals, 2 localities.

Collection sites: Western United States.

Sympatry: *Sceloporus - occidentalis, undulatus*.

References: Ferguson, 1971a, 1971b; Stebbins, 1944; Stebbins and Robinson, 1946; Woodbury and Woodbury, 1939, 1945; Smith, 1946.

### Undulatus Group

#### *Sceloporus cautus*

**Habitat:** Mesquite grassland zone, on ground near brush, terrestrial.  
**Social system:** territorial in nature, dominance and despotism in enclosures.

**DAP (Fig. 7)**

Site: raised area on ground.

Orientation: lateral presentation.

Posture: lateral compression, dewlap.

Body movements: movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.

Sequence: Indeterminate.

Description: A simple series of pushups. U1 - rise to full height, hold, down to low amplitude (0.63), pause (0.19), U2 through U5 similar to U1, U2 (0.69), pause (0.13), U3 (0.94), pause (0.25), U4 (0.56) pause (0.31), U6 - incomplete unit.

Note third unit differs in length from first two units.

Sample: 18 sequences, 2 individuals, 2 localities.

Collection sites: (1) 18 km N of Matahuala, Hw 57, San Luis Potosi, Mexico, Apr. 1, 1966; (2) 20 km N of San Roberto, Nuevo Leon, Mexico. April 1, 1966.

Sympatry: *Sceloporus scalaris*.

References: Bussjaeger, 1971.

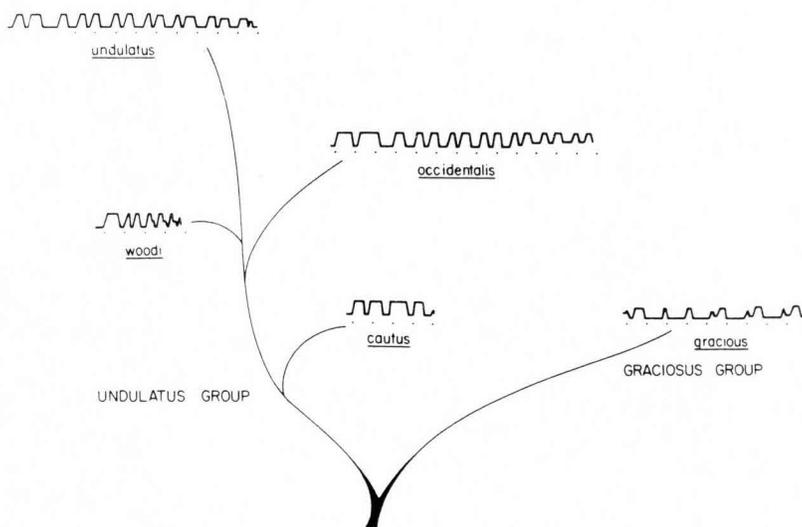


Figure 7. Display-action-pattern graphs of species members of the *undulatus* and *graciosus* groups of *Sceloporus*. Dots below graphs indicate one second intervals in time.

### **Sceloporus occidentalis**

**Habitat:** boulders, logs, wooded rocky areas, hillsides, canyons, fences.

**Social system:** territorial in nature, dominance and despotism in enclosures.

**DAP (Fig. 7)**

Site: raised area.

Orientation: lateral presentation, face off.

Posture: lateral compression, dewlap.

Body movements: movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.  
Ratio, S = 0.834 H = 0.453

Sequence: Indeterminate.

Description: A series of repeated pushups with a repeated pattern varying in cadence. U1 - rise to full amplitude, hold, down (0.94), pause (0.25), U2 through U5 similar, but differing in cadence of pauses and intensity, U2 (1.06), pause (0.63), U3 (0.63), pause (0.44), U4 and U5 (doublet), with short pause between (1.25), pause (0.38), U6 + U7 (doublet) (1.19), pause (0.63), U8 + U9 (doublet) (1.19), pause (0.38), U10 + U11 (doublet), not returning to low amplitude (1.13), pause (0.38), U12 + U13 (doublet) returning to 1/3 amplitude (1.13), pause (0.44), U14 + U15 (doublet) returning to 1/3 amplitude (1.13). (1.13).

Note that the initial two units form a long doublet, U3 is not paired, and all succeeding units appear as doublets.

Sample: 21 sequences, 3 individuals, 3 localities.

Collection sites: (1) San Bernadino County, Calif., Mar. 25, 1963; (2) SW United States, June 1963; SW United States, 1964.

Sympatry: *Sceloporus - graciosus, orcutti*.

References: Fitch, 1940; Gander, 1956; Purdue and Carpenter, 1972a, 1972b, Smith, 1946; Speck, 1924; Stebbins, 1954; Stuart, 1972; Tanner and Hopkin, 1972; Van Denburgh, 1897, 1922; Wood, 1936.

### **Sceloporus undulatus**

**Habitat:** broad habitat spectrum - forests, tree trunks, logs, fences, sand dunes, beaches, wooded ravines.

**Social System:** territorial in nature, dominance and despotism in enclosures.

**DAP (Fig. 7)**

Site: raised area.

Orientation: lateral presentation, face off, tilt, horizontal or vertical.

Posture: lateral compression, dewlap.

Body movements: movements of head, neck and anterior trunk

by 2-legged pushups with extension and flexion of front legs.  
Ratio,  $S = 0.819$   $H = 0.470$

Sequence: Indeterminate.

Description: A series of repeated pushups with a repeated pattern varying in cadence. U1 - rise to full height, hold, down (0.63), U2 through U5 similar, decreasing slightly in height at end of series, U2 (0.75), pause (0.69), U3 (0.50), pause (0.38), U4 + U5 (doublet) with short hold in between (0.19), pause (0.44), U6 + U7 (doublet) (1.19), pause (0.44), U8 + U9 (doublet) (1.19), pause (0.38), U10 + U11 (doublet) (1.19), pause (0.31), U12 + U13 (doublet) (1.19).

Note that the initial first two units form a doublet, the third unit is single, then all succeeding units appear in doublets, decreasing in height slightly (intensity) at the end.

Sample: 113 sequences, 5 individuals, 3 localities.

Collection sites: (1) Little River bridge area between Idabel and Broken Bow, McCurtain County, Oklahoma. June 24, 1970; (2) Southport Development, Lake Eufaula, McIntosh County, Oklahoma. May 1970; Camp Egan area, Cherokee County, Oklahoma. May 2, 1970.

Sympatry: *Sceloporus - couchi, graciosus, jarrovi, olivaceus*.

References: Carpenter, 1962; Ferguson, 1971; Griffith, 1966; Hayes and Carpenter, 1971; Hyde, 1923; Kennedy, 1958; McCauley, 1945; Mertens, 1960; Noble, 1923; Noble and Bradley, 1933; Noble and Teale, 1930; Purdue and Carpenter, 1972a, 1972b; Schmidt and Inger, 1957; Smith, 1946; Smith, 1961; Vinegar, 1972, Yoshida, 1966.

### *Sceloporus woodi*

**Habitat:** rosemary bush scrub, more in "open strands".

**Social system** unknown in nature, dominance in enclosures

**DAP** (Fig. 7)

Site: raised area on ground

Orientation: lateral presentation, face off.

Posture: lateral compression, dewlap, rises on four legs.

Body movements: movements in head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs, or at high intensity there may be action in all four legs.

Sequence: Indeterminate.

Description: A series of pushups with a repeated pattern appearing after the first three units: U1 - rise to full height, long hold, down (0.81), pause, (0.19), U2 - rise to full height, short hold, down (0.31), pause (0.13), U3 - similar to U2 (0.38), pause (0.25), U4 - rise to full height, short hold, down to 1/2 amplitude, short hold, down (0.44), pause (0.13), U5 and U6 similar to U4, U5

(0.50), pause (0.16), U6 (0.44), U7 incomplete.

Note that the initial unit is longer than following units, that U2 and U3 are similar, then the following units are repeats.

Sample: 4 sequences, 2 individuals, 1 locality.

Collection site: Florida, spring 1960.

Sympatry: *Sceloporus undulatus*.

#### Spinusus Group

##### *Sceloporus edwardtaylori*

**Habitat:** savanna, small areas of cleared farmland in open forest, tropical deciduous forest, thorn forest, arboreal.

**Social system:** unknown.

**DAP** (Figure 8)

Site: raised area and in trees.

Orientation: lateral presentation, face off, tilt vertical (preferred) and on horizontal surfaces.

Posture: lateral compression, dewlap, arch back.

Body movements: movements of the head, neck and anterior trunk by 2-legged pushups with extension and flexion of the front legs.

Sequence: Indeterminate

Description. A long series of long hold pushups with suggested pattern. U1 - rise to full height, hold, down to low amplitude (0.63), pause (.156), U2 - through U8 similar, but cadence varies. U2 - (1.19), pause (1.44), U3 (0.88), pause (0.69), U4 (0.44), pause (0.75), U5 (0.50), pause (1.13), U6 (1.19), pause (0.75), U7 at 2/3 full height (0.44), pause (0.38), U8 at 2/3 full height (0.50)

Note pattern of repeated units U3 - U5, and U6 - U8, a pattern of one long and two short pushups.

Sample: 49 sequences, 9 individuals, 2 localities.

Collection sites: (1) 5-14 km S of Tehuantepec, Hw 185, Oaxaca, Mexico. Aug. 21, 1967, Aug. 24, 1968; (2) 5 km N. junction of Hw 190 & 185, Oaxaca, Mexico. Aug. 21, 1967, Mar. 25, 1968.

Sympatry: *Sceloporus siniferus*.

Reference: Bussjaeger, 1971.

##### *Sceloporus melanorhinus*

**Habitat:** tropical deciduous forest, arboreal. Associated with yellow grass trees (*Astianthus viminalis*).

**Social system:** dominance in enclosures.

**DAP** (Fig. 8)

Site: raised area

Orientation: lateral presentation, face off, tilt vertical (preferred) and horizontal surfaces.

Posture: lateral compression, dewlap, arch back.

Body movements: movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.

Sequence: Indeterminate.

Description: A series of long pushups of varying cadence. U1 - rise to full height, long hold, down to low amplitude (1.25), pause (0.81), U2 - U7 similar, but varying in cadence, U2 (0.94), pause (0.44), U3 (1.75), pause (0.50), U4 (1.13), pause (1.19), U5 (1.13), pause (0.31), U6 (0.94), pause (0.31), U7 (1.63).

Note that no repeated or consistent pattern is apparent.

Sample: 151 sequences, 14 individuals, 5 localities.

Collection sites: (1) 10 km E of Manzanillo, Hw 200, Colima, Mexico. Mar. 28, 1967; (2) 13 km E of Zihuatanejo, Hw 200, Guerrero, Mexico, Aug. 18, 1967; (3) 13 - 36 km E of Tepic, Hw 15, Nayarit, Mexico, May 7, 1968; (4) Rio Maralasco, 13 km E of Barra de Navidad, Mexico, Mar. 20, 1968; (5) 4 km S of Colima, Mexico Apr. 21, 1968.

Sympatry: *Sceloporus* - *clarki*, *horridus*, *phyrocephalus*, *uti-formus*.

Reference: Bussjaeger, 1971.

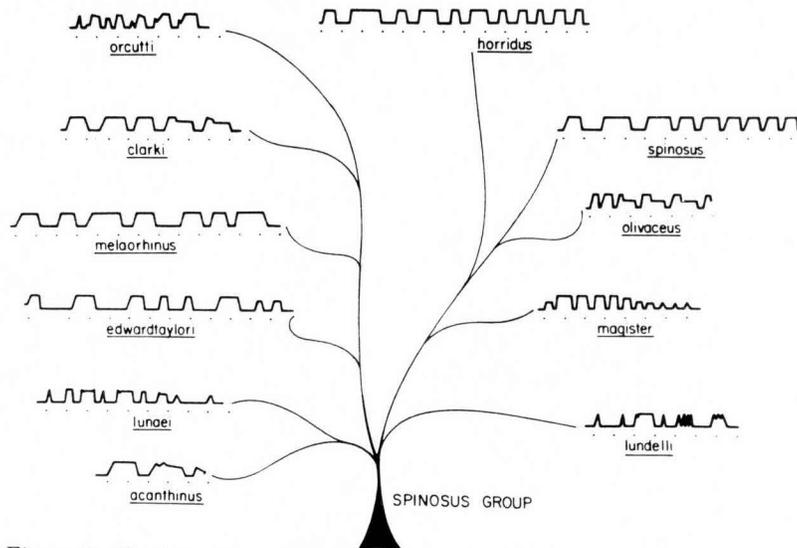


Figure 8. Display-action-pattern graphs for species members of the *spinosus* group of *Sceloporus*. Dots below graphs indicate one second intervals in time.

#### *Sceloporus acanthinus* (*S. a. acanthinus*)

Habitat: log piles, roadside trees, fence posts, small boulders and rocky roadcuts - especially vertical surfaces. Terrestrial and arboreal.

**Social system:** unknown.

**DAP (Fig. 8)**

Site: raised area, usually vertical surface.

Orientation: lateral presentation, face off, tilt; prefer to display from vertical surface.

Posture: lateral compression, dewlap.

Body movements: movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.

Sequence: Indeterminate.

Description: Only short sequences observed, of assertion type. U1 - rise to full height, a long hold, down to low amplitude (1.5 sec), pause (0.50), U2 - rise to full height with jerky stop, slightly descending hold, down to low amplitude (1.81), pause (0.38), U3 - (probably not complete), pushup of lower height, descending and ending at mid-amplitude (0.56).

The notable feature is the length of the first two units.

Sample: 7 sequences, 3 individuals, 1 locality.

Colleciton site: 10 km SW of Retalhuleu, near Hw 95, Guatemala, Apr. 1, 1969.

Sympatry: *Sceloporus variabilis*.

Reference: Bussjaeger, 1971.

**Sceloporus lunaei (S. acanthinus lunaei)**

**Habitat:** trees and logs, boulders, fence posts, arboreal and terrestrial.

**Social system:** unknown.

**DAP (Fig. 8)**

Site: raise area, prefers vertical surfaces.

Orientation: lateral presentation, face off, tilt.

Posture: lateral compression, dewlap.

Body movements: movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.

Sequence: Indeterminate.

Description: A series of irregular pushups with a suggested pattern. U1 - rapid rise to full height and quick lowering to low amplitude (0.25), pause (0.63), U2 - rise to full height with short hold and down to low amplitude (0.44), pause (0.31), U3 - rise to full height with jerky stop, hold, jerk, down to low amplitude (0.75), pause (0.25), U4 - rapid full height pushup (0.19), pause (0.56), U5 - long pushup with jerk at top of rise (0.88), pause (0.31), U6 - fast 3/4 height pushup (0.31), pause (0.50), U7 - 3/4 height pushup with jerk at top of rise, hold, down (0.56), pause (0.50), U8 - rapid 3/4 height pushup (0.38), pause (1.25), U9 - mid-height pushup (0.38).

Note that after the initial unit, the following units appear as a short unit followed by a longer unit, this pattern being repeated

through U7 after which the intensity decreased and patterning is lost.

Sample: 59 sequences, 8 individuals, 3 localities.

Collection sites: (1) 2-5 km SE of Selama, Guatemala, Apr. 3, 1969, (2) 25 mi W of Jutiapa, Nw CAL, Guatemala, Apr. 4, 1969; (3) Jalapa, Guatemala, Apr. 4, 1969.

Reference: Bussjaeger, 1971.

#### **Sceloporus clarki**

**Habitat:** arboreal, but also in brush piles, thorn scrub.

**Social system:** territorial in nature, dominance in enclosures.

**DAP** (Fig. 8)

Site: raised area.

Orientation: lateral presentation, face off, tilt horizontal and vertical surfaces.

Posture: lateral compression, dewlap, arch back.

Body movements: movements of head, neck and anterior trunk by 2-legged pushup with extension and flexion of front legs.

Ratio; S = 0.790 H = 0.314

Sequence: Indeterminate

Description: A series of two types of long hold pushups. U1 - rise to full height, long hold, down (1.13), pause (0.50), U2 and U3 similar, U2 (1.38), pause (0.25), U3 (1.06), pause (0.44), U4 - rise to full height, short hold, down to 3/4 amplitudes, long hold, down to low amplitude (1.40), pause (0.38), U5 similar to U4 (1.44).

Note that U4 and U5 are the same, but differ from U1 - U3.

Sample: 59 sequences, 13 individuals, 3 localities.

Collection sites: (1) 17 - 36 km E of Tepic, Hw 15, Nayarit, Mexico, May 7, 1968; (2) Near Mazatlan, Sinaloa, Mexico, Hw 15, Mexico, 1965; (3) SW United States.

Sympatry: *Sceloporus* - *horridus*, *magister*, *melanorhinus*, *nelsoni*, *utiformis*.

References: Bussjaeger, 1971; Purdue and Carpenter, 1972a, 1972b.

#### **Sceloporus orcutti**

**Habitat:** semi-arid to arid; rock in subtropical thorn forest, oak-pine woodland, chaparral, terrestrial.

**Social system:** dominance in enclosures.

**DAP** (Fig. 8)

Site: raised area

Orientation: lateral presentation, face off, tilt, horizontal or vertical surface.

Posture. lateral compression, dewlap, arch back.

Body movements: movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs,

with slight action in hind legs.

Sequence: Indeterminate.

Description: A series of irregular pushups with a pattern in the latter pushups. U1 - rise to full height and immediately down (0.25), pause (0.19), U2 - rise to 1/4 height, short hold, quick rise to full height, hold, down (0.75), pause (0.19), U3 - rise to 3/4 height, short hold, down (0.31), pause (0.13), U4 - rise to full height, hold down (0.50), pause (0.25), U5 and U6, rise to 1/3 height, quickly down, immediate rise to full height, hold height, hold down (0.81), pause (0.38), U7 - rise to 3/4 height, jerk down and up to full height, hold, down (0.88), pause (0.31), U8 similar to U7 (1.0).

Note that a repeated pattern in U5 plus U6, then U7, U8 or, the entire sequence is of repeated units, a short pushup or jerk, alternating with long hold pushups, with an accelerating cadence throughout the sequence.

Sample: 78 sequences, 14 individuals, 2 localities.

Collection sites: (1) SW United States; (2) Tortuga Island, Gulf of California, Mexico. Aug. 1964.

Sympatry: *Sceloporus - graciosus, occidentalis*.

References: Bussjaeger, 1971, Mayhew, 1963; Purdue and Carpenter, 1972a.

### **Sceloporus lundelli**

**Habitat:** humid to semi-humid; tropical evergreen forest, tropical deciduous forest, thorn forest, arboreal.

**Social system:** unknown.

**DAP** (Fig. 8)

Site: raised area.

Orientation: lateral presentation, face off, tilt from horizontal or vertical (preferred) surfaces.

Posture: lateral compression, dewlap, arch back.

Body movements: movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.

Sequence: Indeterminate.

Description: An irregular series of mostly rapid pushups. U1 - rapid rise to full height and immediately down (0.31), pause (1.0), U2 - rapid rise to full height and immediately down (1.9), pause (0.44), U3 - rapid rise to full height with jerk at top, hold, down (1.06), pause (0.31), U4 - similar to U1 and U2 (0.19), pause (0.50), U5 - through U8 similar to U2 and U4, but with no pauses in between, U5 (0.25), U6 (0.19), U7 (0.19), U8 (0.19), pause (0.88), U9 - rise to full height with jerky hold at top, down (0.69).

Note the appearance of a long pushup preceded and followed by rapid pushups.

Sample: 4 sequences, 1 individual, 1 locality.

Collection site: Progreso, Yucatan, Mexico, May 1969.

Sympatry: *Sceloporus - chrysostictus, cozumelae*.

Reference: Bussjaeger, 1971.

#### **Sceloporus magister**

**Habitat:** semi-arid to arid, subtropical thorn scrub, desert grassland, desert scrub, terrestrial, with arboreal tendencies.

**Social system:** territorial in nature, dominance in enclosures.

**DAP (Fig. 8)**

Site: raised area.

Orientation: lateral presentation, face off, tilt from horizontal and vertical surfaces.

Posture: lateral compression, dewlap, arch back.

Body movements: movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.

Ratio S = 0.677 H = 0.300

Sequence: Indeterminate.

Description: A series of similar pushups, varying in intensity as they end, and thus in height. U1 - rise to 1/2 height, hold, down (0.44), pause (0.13), U2 - rise to full height, hold, down (0.81), pause (0.19), U3 through U5 similar to U2, U3 (0.63), pause, (0.25), U4 (0.56), pause (0.19), U5 (0.44), pause (0.19), U6-U8 similar to previous pushups but decreasing in height, U6 - 2/3 height (0.44), pause (0.19), U7 (0.38), pause (0.13), U8 (0.44), pause (0.25), U9 rise to 1/2 height and immediately down (0.31), pause (0.31), U10 and U11 similar to U9, U10 (0.25), pause (0.31), U11 (0.31).

Note that the sequence is a series of repeated pushups, rapid with decreasing amplitude and slightly faster cadence, probably due to decreasing intensity.

Sample: 47 sequences, 10 individuals, 3 localities.

Collection sites: (1) 4 km W of Silver Springs, Utah. May 11, 1969; (2) 41 km N of Tonapah, Utah. May 11, 1969; (3) SW United States.

Sympatry: *Sceloporus clarki*.

References: Bussjaeger, 1971; Mosauer, 1936; Purdue and Carpenter, 1972a, 1972b; Smith, 1946.

#### **Sceloporus olivaceus**

**Habitat:** open woodland, subtropical thorn forest, live oak woodland, riparian woodland in subtropical thorn scrub and desert grassland, arboreal, with terrestrial tendencies.

**Social system:** territorial in nature, dominance and despotism in enclosures.

**DAP (Fig. 8)**

Site: raised area, arboreal

Orientation: lateral presentation, face off, tilt from horizontal and vertical surfaces.

Body movements: movements in head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.

Sequence: Indeterminate.

Description: U1 - rapid rise to full height, hold, down (0.44), pause (0.06), U2 similar to U1 (0.63), pause (0.19), U3 - rise to full height, short hold, down to 1/2 amplitude, long hold, down (0.94), pause (0.25), U4 and U5 similar to U3, U4 (1.19), pause (0.19), U5 (1.38), pause (0.25), U6 probably incomplete, but starts in same way as U3 through U5.

Note that after U1 and U2 there are repeated units.

Sample: 48 sequences, 4 individuals, 3 localities.

Collection sites: (1) 16 km S of San Marcos, Texas, Hw 81. Apr. 25, 1966; (2) Fort Worth, Texas, June 1966; (3) Dallas, Texas, June 12, 1966.

Sympatry: *Sceloporus undulatus*.

References: Blair, 1960, Bussjaeger, 1971.

#### **Sceloporus spinosus**

**Habitat:** Ubiquitous, arid central plateau of Mexico; mesquite-grassland zone, desert zone; arid to semi-arid cleared low area of pine-oak forest, subtropical savanna, thorn scrub; terrestrial, boulders and fence posts, has some arboreal tendencies.

**Social system:** dominance in enclosures.

**DAP** (Fig. 8)

Site: raised area.

Orientation: lateral presentation, face off, tilt from horizontal and vertical surfaces.

Posture: lateral compression, dewlap, arch back.

Body movements: movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.

Sequence: Indeterminate.

Description: A series of long pushups with increasing cadence. U1 - rise to full height, long hold, down (0.94), pause (0.94), U2 through U9 are all similar to U1 but varying in cadence, U2 (1.50), pause (0.63), U3 (1.31), pause (0.25), U4 (0.88), pause (0.25), U5 (0.94), pause (0.19), U6 (0.81), pause (0.13), U7 (0.81), pause (0.13), U8 (0.69), pause (0.19), U9 (0.69).

Note similarity in all pushups, except for varying lengths they are held, with increase in tempo as the sequence progresses.

Sample: 144 sequences, 21 individuals, 11 localities.

Collection sites: (1) Pyramid of Cholula, Puebla, Mexico, Mar. 29, 1966; (2) SSW of Apizaco on new road to Tlaxcala, Mexico. Mar. 29, 1966; (3) 28 km NW of Pachuca, Hw 85, Hidalgo, Mexico. Mar. 30, 1966; (4) 16 km of San Luis Potosi, Hw 86, San Luis

Potosi, Mexico. Apr.1, 1966; (5) 5 km S of San Luis Potosi, Hw 80, San Luis Potosi, Mexico, Mar. 30, 1967; (6) Balnerio, Tzindejah, Tasquillo, H2 85, Hidalgo, Mexico, Aug. 14, 1967; (7) 6 km S of Tasquillo, Hw 85, Hidalgo, Mexico. Aug. 14, 1967; (8) 16 km S of Ixmiquilpan, Hw 85, Hidalgo, Mexico, Aug. 14, 1967; (9) 3-16 km S of Oaxaca, Mexico. Aug. 20, 1967; (10) 47 km NW of Oaxaca, Oaxaca, Mexico. Mar. 24, 1968; (11) 4-40 km transect N of Ejutla, Hw 175, Oaxaca, Mexico. May 24, 1968.

Sympatry: *Sceloporus - jalapae, maculosus, mucronatus, torquatus*.

Reference: Bussjaeger, 1971.

### **Sceloporus horridus**

Habitat: arboreal and rocky habitats - several kinds of trees, boulder strewn pastures, candelabra cactus, rocky walls, road cuts, inland semi-arid to arid; subtropical savanna, thorn scrub, terrestrial, with arboreal tendencies.

Social system: dominance in enclosures.

DAP (Fig. 8)

Site: raised area

Orientation: lateral presentation, face off, tilt from horizontal and vertical surfaces.

Posture: lateral compression, dewlap, arch back.

Body movements: movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.

Sequence: Indeterminate.

Description: A series of pushups which alternate short and long as they progress. U1 - rise to full height, long hold, down (0.75), pause (0.94), U2 through U11 similar, but vary in length, U2 (1.69), pause (0.56), U3 (1.38), pause (0.31), U4 (1.0), pause (0.44), U5 (0.75), pause (0.19), U6 (0.94), pause (0.38), U7 (0.50), pause (0.13), U8 (0.94), pause (0.25), U9 (0.56), pause (0.13), U10 (0.94), pause (0.31), U11 (0.50).

Note that after the beginning units, there are alternating short and long units.

Sample: 245 sequences, 32 individuals, 16 localities.

Collection sites: (1) 35 km E of Ixtlan del Rio, Hw 15, Jalisco, Mexico. Mar. 26, 1967; (2) 45 km W of Ixtlan del Rio, H2 15, Jalisco, Mexico, Mar. 26, 1967; (3) km N of Cocula, Hw 80, Jalisco, Mexico, Mar. 27, 1967; (4) 35 km N of Union de Tula, Hw 80, Jalisco, Mexico. Mar. 27, 1967; (5) 16 km S of Colima, Hw 10, Colima, Mexico, Mar. 28, 1967; (6) 96 km S of Uruapan, Hw 37, Michoacan, Mexico, Mar. 29, 1967; (7) 37-65 km S of Cuernavaca, Hw 95, Morelos, Mexico, Aug. 16, 1967; (8) 13 km E of Zihuatanejo, Hw 209, Guerrero, Mexico. Aug. 18, 1967;

(9) 33 km W of Ixacur de Matamoros, Hw 140, Puebla, Mexico, Aug. 19, 1967; (10) 13 km S of Cuernavaca, Hw 75, Morelos, Mexico, Mar. 22, 1968; (11) 16 km SE of Cuernavaca, Hw 115, Morelos, Mexico, Mar. 23, 1968; (12) 6 km SE of Cuatla, Hw 140, Morelos, Mexico, Mar. 23, 1968; (13) 17-36 km E of Tepic, Hw 15, Nayarit, Mexico, May 7, 1968; (14) 10 km N of Tecolatlán, Hw 80, Jalisco, Mexico, May 20, 1968; (15) 4 km S of Colima, Colima, Mexico, Apr. 21, 1968; (16) El Cobano, Hacienda El Cobano, Colima, Mexico, Aug. 12, 1968.

Sympatry: *Sceloporus - clarki, dugesii, melanorhinus, nelsoni, pyrocephalus, siniferus, utiformis*.

References: Bussjaeger, 1971.

#### Pyrocephalus Group

##### *Sceloporus pyrocephalus*

**Habitat:** Rocky areas with cover nearby, some on tree trunks.

**Social system:** dominance in enclosures.

**DAP (Fig. 9)**

Site: raised area, infrequently on ground.

Orientation: lateral presentation, face off, tilt.

Posture: lateral compression, dewlap.

Body movements: movements of the head, neck, trunk, and sometimes tail by 4-legged pushups with extension and flexion of both front and hind legs, a forward stretch of body preceding pushups. Ratio  $S = 0.926$   $H = 1.091$

Sequence: Apparently intermediate between Determinate and Indeterminate.

Description: A prolonged series of widely spaced pushups suggesting an alternating pattern. U1 - rise to full height, hold, down to low amplitude (1.0 sec), pause (1.88), U2 = rise to full height, short hold, down to low amplitude (0.56), pause (1.0), U3 - U11 similar but varying in cadence, U3 (0.69), pause (1.63), U4 (0.44), pause (1.19), U5 - with short hold (0.31), pause (0.44), U6 (0.50), pause (0.69), U7 (0.88), pause (1.94), U8 (0.56), pause (1.44), U9 (0.38), pause (0.38), U10 (0.50), pause (1.44), U11 (1.0).

Note that units 4-7, and 8-11, are sets of repeated series of unities, while units 1-3 do not fit this pattern.

Sample: 52 sequences, 7 individuals, 4 localities.

Collection sites: (1) 19 - 24 km SE of Colima, Colima, Mexico, March 28, 1967; (2) 10 km E of Manzanillo, Colima, Mexico, March 28, 1967; (3) 16 km S of Colima, Colima, Mexico, March 28, 1967; (4) 96 km S of Uruapan, Michoacan, Mexico, March 29, 1967.

Sympatry: *Scelloporus - horridus, melanorhinus*.

References: Oliver, 1937; Purdue and Carpenter, 1972a, 1972b.

### **Sceloporus nelsoni**

**Habitat:** rocky outcrops with bushy cover, stone walls, boulders in oak forest.

**Social system:** dominance in enclosures.

**DAP** (Figure 9)

Site: raised area, infrequently on ground.

Orientation: lateral presentation, face off, tilt.

Posture: lateral compression (forms a mid-central sharp keel), dewlap.

Body movements: movements of head, neck, trunk, and tail by 4-legged pushups with extension and flexion of all four legs.

Ratio S = 0.914 H = 1.004

Sequence: Indeterminate

Description: A series of pushups alternating long and short units. U1 - slow rise to full height with short hold, down to 1/2 to 1/4 amplitude, hold, down to low amplitude (1.44 sec), pause (0.56), U2 - rise to 2/3 height and quickly down to low amplitude (0.31), pause (0.38), U3 - a rapid rise to 1/4 to 1/2 height, short hold, continued rise to full height, short hold, continued rise to full height, short hold, down to 1/3 to 1/4 amplitude, hold, quickly down to low amplitude (1.44), pause (0.56), U4 - same as U2 (0.19), pause (0.50), U5 - same as U3 (1.25), pause (0.50), U6 - same as U2 (0.19), pause (0.69), U7 - same as U3 (1.44), pause (0.38), U8 - same as U2 (0.25), pause (0.25), U9 - same as U3 (1.31).

Note that the initial unit (U1) is similar to the long units which alternate with short, rapid, low amplitude pushups. The appearance of the long units is that of a jerk stop on rising and a jerk stop on lowering.

Sample: 51 sequences, 7 individuals, 3 localities.

Collection sites: (1) 6 km inside of border of Nayarit, S of Sinaloa, Mexico. March 31, 1965; (2) 35 km E of Ixtlan del Rio, Jalisco, Mexico. March 26, 1967; (3) 11 km E of La Galinda, Nayarit, Mexico. March 26, 1971.

Sympatry: *Sceloporus - clarki, horridus, uniformis*.

References: MaCaskill and Carpenter, 1965; Purdue and Carpenter, 1972a, 1972b; Yoshida, 1966.

### **Merriami Group**

#### **Sceloporus merriami**

**Habitat:** open rocky areas, hillsides, canyons, large boulders, cliffsides, crevices.

**Social system:** territorial in nature, dominance in enclosures.

**DAP** (Figure 9)

Site: raised areas, prominences, ledges, large boulders, rarely

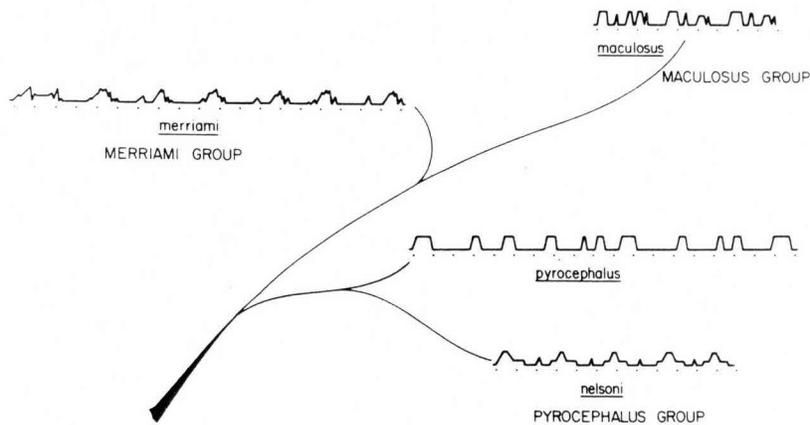


Figure 9. Display-action-pattern graphs for species members of the *pyrocephalus*, *maculosus*, and *merriami* groups of *Sceloporus*. Dots below graphs indicate one second intervals in time.

on ground.

Orientation: lateral presentation, face off, tilt.

Posture: lateral compression (to mid-ventral keel), dewlap

Body movements: movements of head, neck, trunk and tail by 4-legged pushups with extension and flexion of front and hind legs. Ratio S = 0.990 H = 1.549

Sequence: Apparently intermediate between Determinate and Indeterminate.

Description: A series of irregular jerky sequences alternating in the appearance of the first units. S1 - rise to 1/2 height, jerk, continued rise to full height and immediately down to low amplitude and immediate rise to 1/2 height with jerk stop, hold, jerk, then rise to full height and down with jerk at low amplitude (2.25), pause (1.31), S2 - rise to full height jerking twice during rise, jerk at full height, down to 1/2 amplitude and short rise, then down to low amplitude with double jerk (1.5), pause (0.88), S3 - rise to 1/2 height and quickly down, rise to full height with jerk at full height, down with two jerks at low amplitude (1.81), pause (1.31), S4 - similar to S2 (1.25), pause (1.06), S5 - similar to S3 (2.0), pause (0.94), S6 - similar to S3 and S5 (1.56), pause (1.38), S7 - similar to S4 and S6 (1.94).

Note alternating of rapid sequences after the different initial sequence, S2, S4, S6 with jerky rise, and S3, S5, S7 starting with low jerk followed by a hold, then rapid rise with high jerks followed by low jerks.

Sample: 30 sequences, 5 individuals, 2 localities.

Collection sites: (1) Devil's River Bridge, 16 km NW of Del Rio, Val Verde Co., Texas. April 11, 1960; (2) 15 km W of Cuatro

Cienegas, Coahuila, Mexico. March 28, 1969.

Sympatry: *Sceloporus* - none observed.

References: Carpenter, 1961; Chaney and Gordon, 1954; Hunsaker, 1962; Milstead, 1970; Minton, 1958; Purdue and Carpenter, 1972a, 1972b; Smith 1946; Wright and Wright, 1927.

### Maculosus Group

#### *Sceloporus maculosus*

**Habitat:** high desert, volcanic hills and outcrops with crevices, spiny vegetation, cholla, agave, cactus, ocotillo and sparse grass.

**Social system:** unknown.

**DAP** (Figure 9)

**Site:** rock surfaces, near crevices and ledges; mostly on ground in enclosures.

**Orientation:** not observed - assertion displays only.

**Posture:** lateral compression, dewlap.

**Body movements:** movements of head, neck, trunk and tail by 4-legged pushups with and flexion of both front and hind legs. Ratio H = 1.720

**Sequence:** Apparently intermediate between Determinate and Indeterminate.

**Description:** Except for the first series of pushups, appears to be repeated sequences of 4 units. U1 - rise to full height, hold, down to low amplitude (0.56), pause (0.31), U2 - rapid rise to almost full height and quickly down (0.19), pause (0.38), U3 - full height pushup with short hold at top (0.38), pause (0.13), U4 - full height pushup with short hold at top (0.44), no pause but U5 - quick rise to full height and down (0.19), pause (0.88), U6 - rise to full height, long hold, down (0.69), pause (0.19), U7 - rise to full height and immediately down (0.25), pause (0.38), U9 - rise to 3/4 height, hold, down (0.50), no pause but U9 - quick pushup to 3/4 height and down (0.19), pause (0.44), units 10 - 13 a repeat of units 6 - 9, U10 (0.75), pause (0.25), U11 (0.25), pause (0.38), U12 (0.50), no pause, U13 (0.19).

Note that units 6 - 9, and 10 - 13 form repeated sequences and that units 4 and 5 are similar to double units 8 and 9, 12, 13, while units 1 and 2 are similar to units 6 and 7, and 10 and 11.

**Sample:** 24 sequences, 2 individuals, 2 localities.

**Collection sites:** (1) 18 km N of Pedricena, Durango, Mexico. April 1, 1969; (2) 37 km SW of Gomez Palacio, Durango, Mexico. March 21, 1969.

Sympatry: *Sceloporus* - *poinsetti*, *spinosus*.

References: Prudue and Carpenter, 1972b.

## Variabilis Group

### *Sceloporus cozumelae*

**Habitat:** sandy soils and beach scrub area, inland to salt marsh with sparse vegetation, coconut plantations, debris piles near human habitations: terrestrial.

**Social system:** unknown.

**DAP (Figure 10)**

Site: exposed site on ground.

Orientation: lateral presentation.

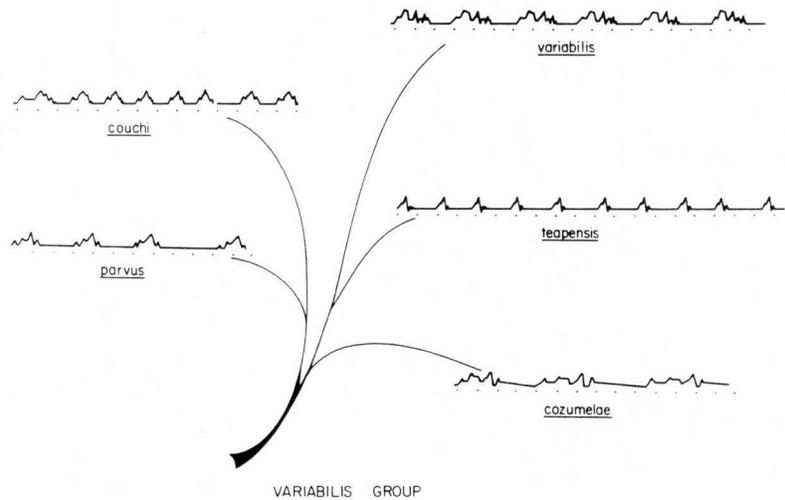
Posture: lateral compression, dewlap.

Body movements: movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.

Sequence: Determinate.

Description: A series of repeated jerky sequences. S1 - rise to 2/3 height with jerk down to 1/2 amplitude, short hold, up to full height, down to 3/4 amplitude, hold, down to 1/4 amplitude, short hold, up to 2/3 then full height and down to low amplitude (2.13 sec), pause, slowly descending to low amplitude (1.88), S2 and S3 similar to S1, S2 (2.88), pause, slowly descending to low amplitude (1.13), S3 (2.94).

Note a series of three repeated sequences which return to low amplitude near end only, with pause starting at mid-height.



**Figure 10.** Display-action-pattern graphs for species members of the *variabilis* groups of *Sceloporus*. Dots below graphs indicate one second intervals in time.

Sample: 25 sequences, 1 individual, 1 locality.  
Collection site: Chicxulub Puerto, near Progreso, Yucatan,  
Mexico. May 1969.  
Sympatry: *Sceloporus - chrysostictus, lundelli*.  
References: Penner, 1970.

#### **Sceloporus couchi**

**Habitat:** discontinuous rocky canyons in low mountains (to highest elevations), desert vegetation, on rocky outcrops or large boulders, terrestrial.

**Social system:** Territorial in nature, dominance or despotism in enclosures.

#### **DAP (Figure 10)**

Site: raised or exposed area on steep hillside.

Orientation: lateral presentation, face off.

Posture: lateral compression, dewlap.

Body movements: movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.

Sequence: Determinate.

Description. A series of repeated jerky sequences which accelerate, then decelerate in cadence. S1 - rise to 2/3 height and down to 1/2 amplitude, hold, up to full height and down with jerks up to low amplitude (1.94), pause (0.69), S2 - S8 similar to S1 with faster cadence, then slowing down, S2 (1.06), pause (0.63), S3 (0.94), pause (0.63), S4 (0.88), pause (0.75), S5 (0.81), pause (0.63), S6 (0.81), pause (1.44), S7 (0.94), pause (0.88), S8 (1.06).

Note repeated jerky sequences with increasing tempo in first part of each sequence, then slowing down.

Sample: 46 sequences, 4 individuals, 1 locality.

Collection site: 18 km SW of Sabinas Hidalgo, Nuevo Leon, Mexico. March 28, 1970.

Sympatry: *Sceloporus undulatus*.

#### **Sceloporus parvus**

**Habitat:** semi-arid regions, on ground, in areas with desert vegetation - cactus, yucca, thickets of grass and shrubs, rocky strewn rolling hills and ravines; terrestrial.

**Social system:** territorial in nature, dominance and despotism in enclosures.

#### **DAP (Figure 10)**

Site: raised site in exposed areas.

Orientation: lateral presentation, face off.

Posture: lateral compression, dewlap.

Body movements: movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.

Ratio S = 0.723 H = 0.322

Sequence: Determinate.

Description: A series of repeated jerky sequences. S1 - rise to 1/3 height and down, up to 2/3 height and down to 1/2 amplitude, short hold, up to full height and down, up to 1/3 height and down (1.37), pause (1.75), S2 - S4 similar to S1, S2 (1.31), pause (1.69), S3 (1.31), pause (2.94), S4 (1.44), pause (0.81), S5 (1.31).

Note each sequence jerks as it ascends, then down quickly with jerk at end.

Sample: 60 sequences, 5 individuals, 2 localities.

Collection sites: (1) 22 km NW of Actopan, Hidalgo, Mexico. March 30, 1966. (2) 36 km SE of Saltillo, Hw 57, Coahuila, Mexico. March 30, 1969.

Sympatry: *Sceloporus - dugesii, poinsetti, scalaris*.

References: Purdue and Carpenter, 1972a, 1972b.

#### *Sceloporus teapensis*

Habitat: cleared areas, margins of wooded areas, pastures, hedge rows and brush piles, thickets of scrub, debris beneath coconut palms; terrestrial.

Social system: territorial in nature, dominance and despotism in enclosures.

#### DAP (Figure 10)

Site: exposed and raised areas near ground or on ground.

Orientation: lateral presentation, face off, tilt.

Posture: lateral compression, dewlap.

Body movements: movements of head, neck and trunk by 2-legged pushups with extension and flexion of front legs. Ratio S = 0.710 and H = 0.269

Sequence: Determinate.

Description: A long series of repeated, short, jerky pushups. S1 - rise to full height with jerk on way up, quickly down to low amplitude and up slightly with two jerks (0.88), pause (1.06), S2 - S10 similar to S1, S2 (0.75), pause (1.31), S3 (0.69), pause (1.38), S4 (0.69), continuing similarly through S10.

Note all are repeated, short, jerky, sequences.

Sample: 75 sequences, 14 individuals, 5 localities.

Collection sites: (1) 13 km W of Bara de San Pedro, Tobasco, Mexico. March 27, 1968; (2) 16 km N of Acuyacan, Veracruz, Mexico. March 28, 1968; (3) 6 km E of San Andres Tuxtla, Veracruz, Mexico. March 29, 1968; (4) 22 km W of Veracruz, Veracruz, Mexico. March 29, 1968; (5) Saloma, 80 km NE of Guatemala City, Guatemala, April, 1969.

Sympatry: *Sceloporus* - none observed.

References: Milstead, 1969; Purdue and Carpenter, 1968, 1972a, 1972b.

### *Sceloporus variabilis*

**Habitat:** sandy coastal area, thorn scrub, old cultivated fields, volcanic and limestone outcrops, rock walls, fence posts, archeological ruins, road cuts, human habitations; terrestrial, but climbs low objects.

**Social system:** territorial in nature, dominance and despotism in enclosures.

**DAP (Figure 10)**

Site: raised areas, exposed, on ground.

Orientation: lateral presentation, face off.

Posture: lateral compression to sharp ventral keel, dewlap, arch back.

Body movements: movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs.

Sequence: Determinate.

Description: A repeated series of jerky sequences. S1 - rise to 1/2 height with jerk stop, up to full height, hold, down to 1/3 amplitude, hold, up to full height with jerk, down to low amplitude, up to 1/3 height, down, up to 2/3 height, and down with jerks to low amplitude (1.81), pause (1.06), S2 - S6 similar to S1, S2 (2.0), pause (1.31), S3 (2.0), pause (1.06), S4 (2.0), pause (1.50), S5 (1.88), pause (1.69), S6 (1.69).

Note the approximately two seconds long sequence, similar in jerky pattern and ending in a jerky manner.

Sample: 86 sequences, 9 individuals, 7 localities.

Collection sites. (1) El Tajin Archeological Ruins, 21 km S of Poza Rica, Veracruz, Mexico. March 26, 1966; (2) 22 km N of Veracruz, Veracruz, Mexico. March 28, 1966; (3) 6 km S of Jalapa, Veracruz, Mexico. March 28, 1966; (4) 14 km SE of Jalapa, Veracruz, Mexico. March 23, 1966; (5) Emilio Carranza and Rio Juhigne, Gulf Road 180, Veracruz, Mexico. March 27, 1966; (6) 1-16 km N of Ixtapa, Hw 195, Chiapas, Mexico. March 26, 1968; (7) 14 km SE of Jalapa, Veracruz, Mexico. March 23, 1970.

Sympatry: *Sceloporus acanthinus*.

References: Purdue and Carpenter, 1972a, 1972b; Ratzlaff and Carpenter, 1966.

### Chrysostictus Group

#### *Sceloporus chrysostictus*

**Habitat:** beach scrub, thorn forest, on sandy and rocky soils.

**Social System:** territorial in nature, dominance or despotism in enclosures.

**DAP (Fig. 11)**

Site. raised area

Orientation. lateral presentation

Posture: lateral compression, dewlap

Body movements. movements of head, neck and anterior trunk by 2-legged pushups with extension and flexion of front legs. Ratio S = 0.721 H = 0.220

Sequence: Determinate

Description: A series of repeated jerky sequences. S1 - rise to 1/2 height, down, hold, rise to 1/2 height, jerk to full height, down to 1/2 amplitude, short hold, down to low amplitude, up to full height with jerk on rise, down to low amplitude, up to 1/2 amplitude and down, up to 1/4 amplitude and down (2.63 sec), pause (1.88), S2 and S3 similar to S1, S2 (2.12), pause (2.56), S3 (2.06)

Note a jerky sequence which is repeated in essentially the same pattern.

Sample. 54 sequences, 5 individuals, 1 locality.

Collection site: Progreso, Yucatan, Mexico, May 1969.

Sympatry: *Sceloporus - cozumelae, lundelli*.

References: Penner, 1970; Purdue and Carpenter, 1972a, 1972b.

### Siniferus Group

#### *Sceloporus siniferus*

Habitat: thorn scrub, old cultivated fields, hedgegrows, open forest scrub.

Social system: territorial in nature, dominance and despotism in enclosures.

DAP (Fig. 11)

Site: raised objects near ground and on ground.

Orientation: lateral presentation, face off.

Posture: lateral compression, dewlap, arch back, rises of all four legs.

Body movements: movements of head, neck and trunk by 2-legged pushup with some action in hind legs, by extension and flexion. Ratio S = 0.870 H = 0.908

Sequence: Indeterminate.

Description: A series of pushups in which the units appear as groups of three. U1 - rise to 1/2 height, hold quick rise to full height, down (1.06 sec), pause (0.19), U2 - rise to full height, slightly decreasing hold, down (0.38), pause (0.19), U3 - rise to 1/2 full height, short hold, down (0.63), pause (0.31), the remaining units appearing as triplets of pushups with the first pushup of

each triplet being slightly faster than the remaining two, the tempo of the triplets slowing down as they proceed, U4-6, (1.19), pause (0.56), U7-9 (1.50), pause (0.69), U10-12 (2.13), pause (0.69), U13-15 (2.13).

Note that the pattern is of repeated groups of three units, the first three differing from the following triplet groups. The display-action-pattern could be considered Determinate if all actions are considered as a sequence.

Sample: 104 sequences, 13 individuals, 3 localities.

Collection sites: (1) 5 km N of junction of Hw 185 and 190, N of Tehuantepec, Oaxaca, Mexico. Mar. 25, 1968; (2) 5-14 km S of Tehuantepec, Oaxaca, Mexico. Mar. 24, 1968; (3) 48 km S of Oaxaca, Oaxaca, Mexico. May 24, 1968.

Sympatry: *Sceloporus* - *edwardtaylori*, *horridus*, *utiformis*.

References: Purdue and Carpenter, 1972a, 1972b; Sanderford and Carpenter, 1968.

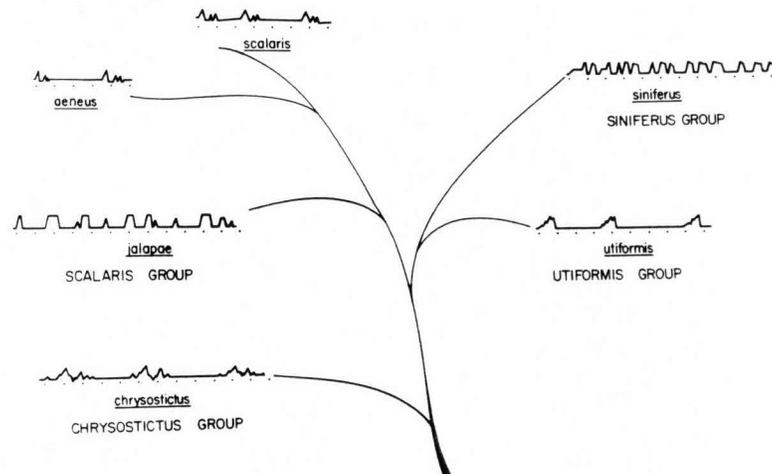


Figure 11. Display-action-pattern graphs for species members of the *chrysostictus*, *scalaris*, *utiformis*, and *siniferus* groups of *Sceloporus*. Dots below graphs indicate one second intervals in time.

### Utiformis Group

#### *Sceloporus utiformis*

Habitat: stumps and logs in oak forest areas, dense brush.

Social system: Unknown.

DAP (Fig. 11)

Site: raised area and on ground.

Orientation: lateral presentation.

Posture: lateral compression, dewlap.

Body movements: movements of the head, neck and trunk by 4-legged pushup with extension and flexion of front and hind legs. Ratio S = 0.909 H = 0.909.

Sequence: Determinate.

Description: A series of repeated short sequences, S1 - slight rise, jerk, continued rise, jerk, rise to full height with jerk at top, down (0.94), pause (2.44), S2 and S3 similar, S2 (0.88), pause (3.63), S3 (0.94).

Appear as rapid pushups which are jerky as lizard rises, then quickly lowers.

Sample: 43 sequences, 1 individual, 1 locality.

Collection site: 32 km E of Tepic, Hw 15, E of Santa Maria del Oro junction, Nayarit, Mexico, May 14, 1968.

Sympatry: *Sceloporus - clarki, horridus, melanorhinus, nelsoni, siniferus*.

References: Belcher and Carpenter, 1968; Purdue and Carpenter, 1972a, 1972b.

### Scalaris Group

#### *Sceloporus aeneus*

**Habitat:** open areas with thick grass clumps, grassy areas in open pine forest.

**Social system:** live in dense colonies; dominance in enclosures.

**DAP** (Fig. 11)

**Site:** on ground or in bunch grass, infrequently on raised area near ground.

**Orientation:** lateral presentation, face off.

**Posture:** lateral compression, dewlap.

**Body movements:** movements of the head, neck and anterior trunk by 2-legged pushups with most action in head region.

**Sequence:** Determinate.

**Description:** A series of rapid and repeated sequences of three units each. S1 - rapid rise from 1/3 height to full height with immediate lowering to low amplitude, short hold, rapid rise to 1/2 height and down, jerky back up to 1/3 height and down with rise up to 1/2 height (0.69 sec), pause (2.88), S2 similar to S1 (1.0).

Note that sequences are rapid and jerky and may appear as head bobbing.

**Sample:** 16 sequences, 7 individuals, 2 localities.

**Collection sites:** (1) 1 km E of Perote, Veracruz, Mexico. Mar. 23, 1970; (2) 5 km W of Las Vegas, Veracruz, Mexico. Mar. 23, 1970.

**Sympatry:** *Sceloporus - cryptus, formosus, grammicus, poinsetti*.

### **Sceloporus scalaris**

**Habitat:** arid areas at high elevations with bunch grass, steep mountain sides with areas of bunch grass.

**Social system:** live in dense colonies; dominance in enclosures.

**DAP (Fig. 11)**

**Site:** on ground, infrequently on raised areas near ground, or on bunch grass.

**Orientation:** lateral presentation, face off.

**Posture:** lateral compression, dewlap.

**Body movements:** movements of head, neck and anterior trunk by 2-legged pushups, with most action in head region. Ratio  $S = 0.819$   $J = 0.436$ .

**Sequence:** Determinate.

**Description:** A series of rapid and repeated sequences of three units each. S1 - rapid rise from 1/2 height to full height and immediately down to low amplitude, hold, rapid rise to 2/3 height and down, very short hold, rise to 2/3 height and down (1.06 sec), pause with slight rise (1.25), S2 similar to S1 and S2 (0.94).

Note that sequences are rapid and jerky and may appear as head bobbing. The cadence increases slightly with each successive sequence.

**Sample:** 76 sequences, 10 individuals, 3 localities.

**Collection sites:** (1) 32 km E of Tepic, Nayarit, Mexico. May 14, 1968; (2) 51 km N of Uruapan, Michoacan, Mexico. Mar. 28, 1969; (3) Barefoot Mountain, Chiracahua Mountains, Cochise County, Arizona. April 3, 1969.

**Sympatry:** *Sceloporus - cautus, dugesii, jarrovi, parvus, poinsetti*.

**References:** Belcher and Carpenter, 1968; Loring and Carpenter, 1972a, 1972b.

### **Sceloporus jalapae**

**Habitat:** high oak-grassland, areas with scattered slab limestone, grass clumps.

**Social system:** territorial in nature, dominance and despotism in enclosures.

**DAP (Fig. 11)**

**Site:** on ground

**Orientation:** lateral presentation, dewlap.

**Posture:** lateral compression, dewlap, arch back.

**Body movements:** movements of head, neck, trunk and tail by 4-legged pushups with extension and flexion of front and hind legs. Ratio  $S = 1.021$   $H = 1.279$

**Sequence:** Determinate.

**Description:** An irregular series of low and high pushups singly and in doublets, with a suggested pattern. U1 - rise to full height,

short hold, down (0.31), pause (1.25), U2 - rise to full height, long hold, down (0.75), pause (0.81), U3 and U4, rise to 1/2 height and down, short hold, rapid rise to full height, hold, quickly down (0.75), pause (0.75), U5 rapid to 3/4 height and quickly down (0.25), pause (0.88), U6 similar to U2 (0.56), pause (0.50), U7 and U8 similar to U3 and U4 but reversed (0.75), pause (0.75), U9 similar to U5 (0.31), pause (1.0), U10 similar to U2 and U6 (0.69), pause (0.38), U11 and U12 similar to U7 and U8 (0.75).

Note that a suggested repeated pattern of 4 units is apparent, as follows: U1 and U2 plus U3 and U4, similar to U5 and U6 plus U7 and U8, except that the pattern of U7 and U8 are reversed from U3 and U4, then U9 and U10 plus U11 and U12 are similar to the appearance of U5 through U8.

Sample: 101 sequences, 8 individuals, 3 localities.

Collection sites: (1) 66 km SE of Tamazulapan, Oaxaca, Mexico. March 23, 1968; (2) 40 km NW of Oaxaca, Oaxaca, Mexico. March 23, 1968; (3) 50 km W of Orizaba, Veracruz, Mexico, March 23, 1968; (4) 34 km S of Yanhuitlan, Oaxaca, Mexico.

Sympatry: *Sceloporus - mucronatus, spinosus, torquatus*.

References: Belcher and Carpenter, 1968; Purdue and Carpenter, 1972a, 1972b.

#### Discussion

Behavior patterns are only a single aspect of a lizard's adaptation to its environment. These behavior patterns are, at least in part, genetically determined and a product of its phylogenetic evolution. Therefore, these behavior patterns should possess some characteristics which indicate relationship at the specific, generic and higher categories.

The differences in behavioral patterns will be related to a lizard's position in its biotic community as a function of its 1) size, 2) sex, 3) age, 4) social system, 5) habitat niche, and 6) sympatry with possible competitors.

The comparative approach used herein brings to light behavior characteristics which, if a species were studied independently, might not be recognized, or if observed would seem trivial and be ignored. Such characteristic differences, seemingly minor, may be intimately united to specific morphological and physiological adaptations (i.e., cryptic coloration, resting posture and site selection) and therefore, influence an individual's survival and the evolution of the species (population).

I have used the comparative approach to study *Sceloporus* in order to determine which and how behavior characteristics 1) indicate relationships with conspecifics, 2) exhibit adaptations to habitat niche, 3) relate to the local social organization of a population, and 4) may maintain reproductive isolation between sympatric conspecifics.

### Social Organization

The social organization of *Sceloporus* possesses great similarity interspecifically and is generally shared with the other iguanid genera. Territoriality is widespread in iguanid lizards and is highly developed in *Sceloporus* forming the basis for the social structure of its species (Carpenter, 1967a).

The male (*Sceloporus*) declares and defends his territory by performing aggressive (assertion and challenge) displays. These consume much of his time and energy. Though females and juveniles may also exhibit these displays (varies with the species), the displays are of only minor importance in determining social structure. In some *Sceloporus*, the degree of social tolerance permits aggregations of ten or more adult individuals whereas in others, males are intolerant, especially of other males, and are spread widely through the available habitat. Commonly a male *Sceloporus* (in many species) shares his home range with one or more females. This type of association is called a harem (Carpenter, 1967a; Kennedy, 1958; Milstead, 1970).

When a group of conspecifics are held in an enclosure the available space usually equals no more than the space used for a single territory in nature. The social response under such conditions is still territorial, but since the equivalent of one territory, or less, is available, the most "successful" male becomes dominant over all other individuals present and declares and maintains his position, as he would in a natural territory, by aggressive displays. He may "subjugate" ten or more males. If removed, another male quickly assumes dominance (dominance shift) and may maintain this dominance or lose it when the former dominant is returned to the enclosure. Because a dominant male in an enclosure situation has such total dominance, I have called such an individual a "despot" and the social structure "despotism". Instances of shared social dominance have been recorded (Carpenter, 1961; Milstead, 1970) but these are the exception rather than the rule.

An enclosed group of *Sceloporus* is artificial and thus the despotism is a result of this non-natural assemblage. However, for the purpose of comparing species, it does allow the gathering of much pertinent data. Many species of *Sceloporus* have been observed displaying in natural situation and I am convinced that the display patterns are unaltered by the captive conditions of the enclosure.

### Aggressive Displays

The aggressive displays of the species of *Sceloporus* are species-specific and involve the performance of time-motion co-ordinated sequences of pushups and head nod actions (DAPs). These sequences, the display-action-patterns, are performed with the lizard

assuming characteristics postural changes and body orientations. With respect to such performances. *Sceloporus* exhibits typical iguanid characteristics (Carpenter, 1967a).

However, the properties of these aggressive displays, in particular the display-action-patterns, differ in important ways between species, and when compared show possible phylogenetic relationships and at the same time adaptations to the environment.

Most species of *Sceloporus* display from raised sites with a wide view of the surrounding area, which is expected because of the territorial nature of the display - to broadcast the male's presence. The site and the orientation of the displaying lizard relate to habitat niche. Those which are arboreal may readily display in a vertical stance on the side of a log or object (tree trunk) as well as horizontal, or any variation in between. Those species which are more terrestrial usually display from a horizontal, or near horizontal site. The saxicolous forms prefer to display from raised sites on a rocky surface. When a male is challenging, he presents himself laterally towards his adversary, and at close range assume the face off orientation, an iguanid characteristic.

Though all species of *Sceloporus* posture in association with the aggressive display in the same way (in particular the challenge display), that is, by extending the dewlap and compressing laterally the sides of the trunk, and often arching the back, the elaboration of the posture varies between species and appears to be related to the general morphology of the species. The large species in the *torquatus* group show relatively less gular extension and degree of lateral compression, while exhibiting more bloating or inflating of the trunk, than the smaller forms such as those in the *variabilis*, *siniferus*, and *grammicus* groups. Considering that the species in the *torquatus* group are crevice dwellers and prone to inflate or bloat themselves within these cavities as a protective measure against predators, such bloating during display may impose morphological limitations on their ability for lateral compression.

Though dewlap extension and lateral compression bring into view the sexual dimorphic male colors present on most species of *Sceloporus*, such behavior is also characteristic of forms not have such coloration (or very poorly developed), i.e., *S. siniferus*, *S. cozumelae* and *S. horridus albiventris* (color very pale if present at all). This color dimorphism may have been secondarily lost while the display posturing has been maintained. In forms such as *S. siniferus*, *S. teapensis* and *S. variabilis*, the lateral compression is extreme with mid-ventral line becoming keel-like.

#### **Intragroup Comparisons**

##### **Formosus Group (two species - *asper*, *formosus*)**

Because of the uncertainty of the group to which *S. acanthinus*

and *S. lunaei* belong (Smith, 1939; Bussjaeger, 1971) they are mentioned in this group while they are placed with the DAP graphs of the *spinosus* group (Figs. 5,8). The DAPs of these four forms differ with *S. formosus* and *S. acanthinus* showing similarities and *S. asper* and *S. lunaei* showing similarities. All four forms have displays that are indeterminate. *S. formosus* and *S. acanthinus* have repeated long units. The third unit of *S. formosus* exhibits a peculiarity in that it is held at full amplitude, then at 1/2 amplitude before returning to low amplitude, and the following units jerk at the end of the rise of each. This pattern is suggested in the *S. acanthinus* display. The irregular and more rapid units of *S. asper* and *S. lunaei* suggest a similarity between these two species.

#### Megalepidurus Group (two species - *megalepidurus*, *cryptus*)

The DAPs of the two forms of this group which were recorded differ markedly (Fig. 5). *S. megalepidurus* has an irregular, indeterminate, display of short units, while *S. cryptus* performs long units, which are quite similar, the sequence also being indeterminate. On the basis of the DAP, the presence of these two species in the same group should be reexamined.

#### Grammicus Group (one species - *grammicus*)

The DAP of this species is distinct and has initial units which differ from the repeated following short sequences which are determinate (if considered sequences) or indeterminate if considered repeated doublets (Fig. 5), or perhaps represent an intermediate stage between determinate and indeterminate.

#### Torquatus Group (six species - *torquatus*, *mucronatus*, *poinsetti*, *ornatus*, *dugesii*, *jarrovi*).

The DAP of the species in this large group vary considerably between species but have in common a jerkiness in their displays (Fig. 6). The three species belonging to the large scaled forms of this group, *S. torquatus*, *S. mucronatus* and *S. poinsetti*, appear to have two characteristics in common; prolonged units which are followed by rapid lowering to low amplitude, often very low amplitude (deep dip), and the pattern of each of these three has an initial unit differing from their following units. *S. torquatus* and *S. mucronatus* appear to have a repeated pattern without pauses in between, while *S. poinsetti* always performs one sequence and then stops with rapid descending shallow bobs or jerks. The small scaled forms, *S. ornatus*, *S. dugessii* and *S. jarrovi*, exhibit shorter sequences, which in *S. dugessii* and *S. jarrovi* are repeated in an indeterminate manner. The display of *S. ornatus* appears most similar to the display of those of the large scaled forms.

When these DAPs (Fig. 6) are compared to those of Hunsaker (1962) for the *S. torquatus* group, it is obvious to me that Hunsaker had seen primarily assertion displays in which the patterns would be much more difficult to discern, especially for *S. mucronatus*, *S. poinsetti* and *S. jarrovi*.

**Graciosus Group** (one species - *graciosus*)

The DAP of this species is indeterminate and exhibits similarity to members of the *S. undulatus* group (Fig. 7)

**Undulatus Group** (4 species - *undulatus*, *occidentalis*, *cautus*, *woodi*).

The DAPs of the species in this group are all similar (Fig. 7). The displays of *S. undulatus* and *S. occidentalis* are essentially the same in all characteristics, with only slight differences in cadence. Only short sequences of *S. cautus* were recorded, but the initial units are similar to *S. undulatus* and *S. occidentalis* in exhibiting two units of similar cadence followed by a pause and unit of slightly different cadence. *S. woodi* also shows this initial pattern, but the following units do not appear as doublets as in *S. undulatus* and *S. occidentalis*, but as single units which present a jerk stop on descent from high amplitude to low amplitude, these following units being repeated, however, as are the doublets of *S. undulatus* and *S. occidentalis* displays. All have indeterminate displays. On the basis of the DAPs, these four species show strong affinities.

**Spinosus Group** (9 species - *lundelli*, *magister*, *olivaceus*, *spinus*, *horridus*, *edwardtaylori*, *melanorhinus*, *clarki*, *orcutti*)

The DAPs of this group are all indeterminate and are, for the most part, similar in having units with a long cadence (Fig. 8). *S. spinosus*, *S. horridus*, *S. edwardtaylori* and *S. melanorhinus* show the greatest degree of similarity. *S. spinosus* and *S. horridus* both exhibit increasing cadence as the sequence proceeds. Both *S. edwardtaylori* and *S. melanorhinus* have patterns which suggest alternating series of units. *S. lundelli* has a pattern least like the patterns of the rest of the group. *S. majister* performs pushups that are simple and at a rapid cadence. *S. clarki* and *S. olivaceus* exhibit similarity in their patterns, the initial two or three being simple pushups, whereas the following units have long holds as they descend from a hold at high amplitude. *S. orcutti* is unique to the group having units which start in a jerky manner. With the exception then of *S. lundelli*, these species appear to form a

natural group with respect to their DAPs.

**Pyrocephalus Group** (two species - *pyrocephalus*, *nelsoni*)

The DAPs of these two species are very different from one another (Fig. 9). The display sequence of *S. pyrocephalus* has a slow irregular cadence of widely spaced pushups which are simple units without any jerks. The display sequence of *S. nelsoni* alternates between a long unit held both on the way up to a hold at high amplitude and on the way down, and a rapid pushup of low amplitude. The sequences of both species are indeterminate.

On the basis of the DAPs, these two species would not appear to be closely related phylogenetically.

**Merriami Group** (one species - *merriami*)

The DAP of this species exhibits both determinate and indeterminate characteristics (Fig. 9). The sequences are very jerky and appear to alternate, one type being preceded by a low amplitude rapid pushup, followed by a pause, which in the alternating type has the low amplitude rapid pushup immediately preceding the longer portion of the sequence. The initial sequence differs from the sequences which follow it. The sequences are performed as a 4-legged pushups.

**Maculosus Group** (one species - *maculosus*)

The DAP of this species differs from all other species (Fig. 9). With the exception of the initial units, the following units appear in a repeated manner and at least the repeated portion of the sequences are indeterminate.

**Variabilis Group** (five species - *cozumelae*, *couchi*, *parvus*, *teapensis*, *variabilis*)

The DAPs of the five species in this group are all repeated jerky sequences which are determinate, but each having its own species-specific pattern (Fig. 10). The differences appear in the number of units per sequence and the temporal or cadence relationships of these sequences. The times for the performance of a typical sequence for each species is as follows:

*cozumelae* - 2.3 seconds  
*variabilis* - 1.9 seconds  
*parvus* - 1.6 seconds  
*couchi* - 1.1 seconds  
*teapensis* - 0.7 seconds

The sequences, especially in *S. teapensis*, *S. variabilis* and

*S. couchi*, may be repeated up to ten for fifteen times in succession, and with pauses of more than one second, produce long performances. With the exception of *S. teapensis* the other four species show cadence variation in the initial unit of each sequence, which affects the cadence of the sequences as a whole, that is, accelerating and decelerating.

A particular unit of similarity between these forms appears to be the third unit of *S. cozumelae*, the first unit of *S. teapensis*, the third unit of *S. variabilis* and the second unit of *S. couchi*, for all show a jerk (inflection on the DAP graph) on the upward motion of the pushup. The third unit of *S. parvus* may be homologous to these, but shows no jerk inflection. In all forms these units are followed by a pushup (or jerk) of at least one unit of lower amplitude.

Placing these DAPs in the context of natural populations, allopatry and sympatry; the two most similar forms morphologically, *S. teapensis* and *S. variabilis* are sympatric in a part of their ranges. The DAPs of these two are very different and could act as effective isolating mechanisms. In enclosures, however, males of both species will court females of the other - the females of these two forms are very similar in appearance. I did not test to see if females discriminate between male types.

Of the five species in the group, *S. variabilis* is the "generalist", it has the widest range and lives in the greatest variety of habitats. Its SAP appears to be the most complex which may contribute to its effectiveness as a communication signal to its own species and not with others. The ranges of *S. parvus* and *S. couchi* and sympatric with *S. variabilis*, however, effective separation may be partially dependent upon other factors than differences in the DAPs. *S. parvus* is much smaller than *S. variabilis* and more of a ground dweller with more habitat restrictions than *S. variabilis*. *S. couchi* is a "specialist" in habitat selection, and this with its distinct DAP would contribute to effectively isolating these forms from both *S. variabilis* and *S. parvus*.

#### **Chrysostictus Group (one species - *chrysostictus*)**

The DAP of this species is distinct and exhibits strong similarities with the species in the *variabilis* group (Fig. 11).

#### **Siniferus Group (one species - *siniferus*)**

The DAP of this species is indeterminate with initial units differing from the following units which appear as triplets (Fig. 11); however, the initial units appear as a triplet also, and the cadence appears to decelerate as the performance proceeds. The DAP differs from all other species observed.

#### Utiformis Group (one species - *utiformis*)

The DAP of this species differs from all other species of *Sceloporus* (Fig. 11). It is a short, jerky ascending sequence which is repeated, after a pause, and is thus determinate. This DAP is very similar to the displays of *Uta stansburiana* (Carpenter, 1962b).

#### Scalaris Group (three species - *aeneus*, *scalaris*, *jalapae*)

The DAP of *S. aeneus* and *S. scalaris* (Fig. 11) are very similar; they differ only in the cadence of their patterns. *S. jalapae* was placed in the *S. scalaris* group by Smith (1939) even though he recognized that this species was not closely related to their members of the group. The DAP of *S. jalapae* is very different from those of *S. aeneus* and *S. scalaris*, and this difference is increased in that *S. jalapae* performs its pushups with all four legs, the other two species using only the front legs. *S. aeneus* and *S. scalaris* are determinate, *S. jalapae* is also to be considered determinate because of the repeated pattern, with one doublet reversal.

#### Intergroup Comparisons

When the DAPs of certain species representing different groups are compared, similarities suggest some close relationships.

The jerky sequences of *S. merriami* (*merriami* group), with the presence of a low amplitude unit preceding or at the start of a sequence, are very similar to the displays of the species in the *variabilis* group, in particular *S. couchi*, which also is very similar in general appearance and habitat preference to *S. merriami*, *S. couchi* ranging in between two races of *S. merriami* (Fig. 12).

*S. chrysostictus* also has a DAP which has jerky sequences with a low amplitude pushup with a pause preceding the long portion of the sequence, and its geographical range, which is adjacent to and continuous with that of *S. teapensis*, suggests a close relationship to the *variabilis* group and the *merriami* group (Fig. 12).

The species in the *formosus* (Fig. 5) and *spinosus* (Fig. 8) groups have DAPs which suggest a close relationship. The display of *S. formosus* and *S. acanthinus* have long hold pushups similar to the majority of the species in the *spinosus* group, and the

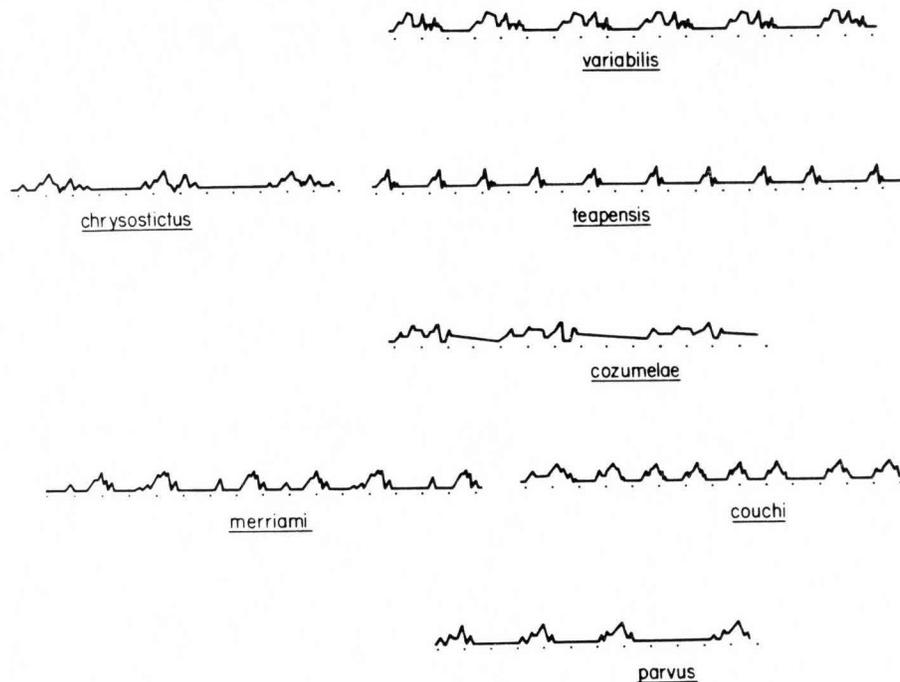


Figure 12. Comparisons of the display-action-patterns of species members of the *variabilis*, *chrysostictus* and *merriami* groups. See discussion.

third unit of the sequence of *S. formosus* is similar to the third and following units of *S. olivaceus* and the fourth and fifth units of *S. clarki*. The display of *S. lundelli*, with rapid pushups interspersed with longer pushups, is similar to the patterns of *S. asper* and *S. lunaei* (in particular).

The DAP of *S. cryptus* (Fig. 5) shows strong similarities to both the *formosus* and *spinosus* groups with its pattern of long hold pushups.

When the DAPs of the species in the *undulatus* group (Fig. 7) are compared to the *formosus* group, *S. cautus* is the most similar, but *S. undulatus* and *S. occidentalis* (which are very similar to each other and have a repeated pattern of doublets) are also similar to the *spinosus* group forms, in particular *S. spinosus* and *S. horridus*, the latter two having slower cadences. *S. graciosus* (Fig.

7) appears to be closely related to the *undulatus* group having initial units followed by doublets as in *S. undulatus* and *S. occidentalis*.

On the basis of the DAPs, a close relationship is suggested between the *formosus* group, *spinosus* group, *undulatus* group and *graciosus* group.

Smith (1939) indicates that the *grammicus* and *megalepidurus* groups as being closely allied to the *formosus* group. The DAP of *S. cryptus* (*megalepidurus* group) shows such a relationship, but *S. megalepidurus* and *S. grammicus* do not. It is my belief that the position of *S. cryptus* in the *megalepidurus* group should be reexamined for a closer relationship to the *formosus* group.

The *torquatus* group (Fig. 6) with respect to the DAPs, appears somewhat homogeneous and does not exhibit much in common with other groups.

The *S. maculosus* and *S. jalapae* (*scalaris* group) have been placed in separate groups (Fig. 13), their DAPs appear to be of the same type, both are small species (52 mm and 56 mm in snout-vent length respectively), terrestrial and perform 4-legged pushups. Whether this indicates a close relationship or not is conjecture, but should be considered when compared by other means.

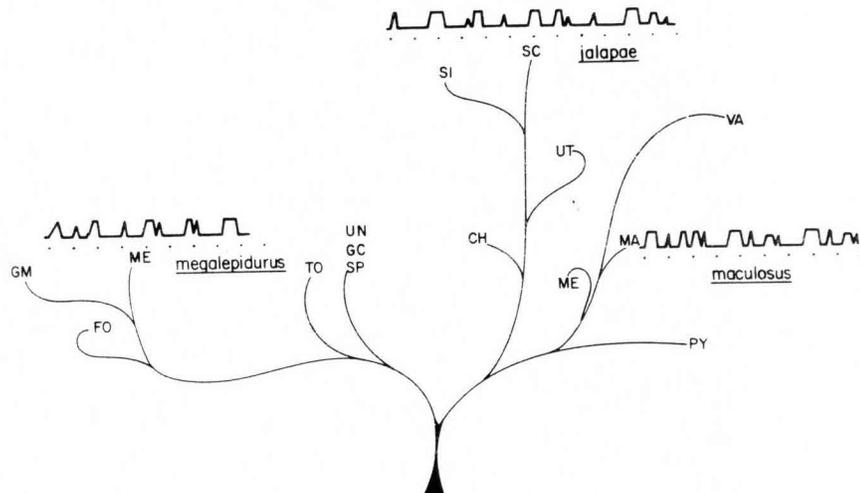


Figure 13. Comparison of display-action-patterns of *S. maculosus*, *S. megalipedurus*, and *S. jalapae*. See discussion.

#### Sympatry Among Sceloporus.

Many species of *Sceloporus* have been observed living in close

association in the field by my students and myself. When comparing the DAPs of closely associated forms, this can be done for species within the same group and in different groups. Many examples of sympatry between species from different groups of *Sceloporus* exhibit marked differences in size and DAPs, as well as habitat preference, and will not be considered here, i.e., members of the *scalaris* group sympatric with species of the *torquatus* group, or *S. siniferus* and *S. utiformis* sympatric with species in the *spinus* group. There are a few examples where sympatric species are of similar size and habitat occupancy and could be expected to encounter one another.

A striking and puzzling example is the closeness of *S. formosus* and *S. cryptus*. These two forms closely overlap each other in the highlands of Oaxaca, Mexico and surprisingly have quite similar DAPs. The important difference appears in the third unit of *S. formosus* which has a consistent half amplitude hold. I suggest a complex relationship between these two very similar species. I further suggest *S. cryptus*, behaviorally, is more closely related to the *formosus* group of species than to *S. megalepidurus* in whose group it has been placed.

The DAPs of two smaller species, *S. grammicus* and *S. aeneus*, also found sympatrically with *S. formosus* and *S. cryptus*, have a much different display pattern and more rapid cadence that may effectively function as an isolating mechanism. *S. grammicus* and *S. aeneus* have different habitat preferences (logs and tree trunks vs. grass dwelling respectively) and *S. aeneus* is a slightly smaller species.

Within the *torquatus* group a number of sympatries occur - *S. jarrovi* - *S. mucronatus*, *S. jarrovi* - *S. poinsetti*, *S. dugessi* - *S. torquatus*, *S. torquatus* - *S. mucronatus*. Since the size and habitat niche preference of these forms are very similar, the display characteristics may play an important role in isolating these forms. The DAPs of *S. dugessi* and *S. jarrovi* (both small scaled) are quite distinct from the large scaled members of this group with which they are found, sympatrically. The displays of *S. mucronatus* and *S. torquatus*, though distinct, show enough similarity that the displays alone may not be effective as an isolating mechanism.

Hunsaker (1962) presented display-action-patterns for the species of the *torquatus* group, which are only suggestive of the DAPs which are presented in this paper. I believe this difference is primarily due to the manner in which Hunsaker obtained his data, that is, in rather confined cages (144 x 86 cm) where social systems would be difficult to develop. My experience with these species in this particular group has indicated they are very shy or "spooky" and tend to seek cover whenever an observer was pres-

ent. My data were gathered in the large enclosures (equipped with a blind) or in a large environmental chamber through a port equipped with a one-way mirror, and the photographed displays analyzed with the Vanguard Motion Analyzer (not available to Hunsaker). I suggest that what Hunsaker observed and described were primarily low intensity assertion displays and thus might not give the full pattern of the challenge display. Hunsaker also described these displays as head-bobbing with some action in the front legs, which by their intensity would indicate primarily assertion displays.

Hunsaker (1962), however, also ran a series of choice experiments where the female was given the opportunity of choosing a male of its own species as against a male of another species from within the *torquatus* group (supposedly choosing the male which asserted correctly) and also similar experiments where the female chose a model simulating the DAP (his described pattern) as against other patterns. His results indicated that the females chose their own species more than other displays. Perhaps if the full display had been performed, the selection would have been even more positive. Hunsaker's results suggest that the DAPs are important as an isolating mechanism and I concur.

Similarly, sympatry is present between certain species in the *spinosus* group, *S. melanorhinus* - *S. horridus*, *S. melanorhinus* - *S. clarki*, *S. clarki* - *S. magister*, *S. clarki* - *S. horridus*. The DAPs of *S. clarki* and *S. magister* differ from each other and from those of *S. horridus* and *S. melanorhinus* to such a degree that they may function effectively in proper species identification and as an isolating mechanism. However, the DAPs of *S. melanorhinus* and *S. horridus* differ only slightly in cadence. These species might have difficulty in species identification based upon the display patterns alone. The problem of competition and reproductive isolation between these two in the field poses a challenging problem for study. A significant character may be the striped dorsal pattern of *S. horridus* and the uniform dorsal pattern of *S. melanorhinus*. *S. melanorhinus* is stated to be more arboreal than *S. horridus*.

The similarity in the jerky DAPs of *S. cozumelae* and *S. chryso-stictus*, which are sympatric in Yucatan, may indicate a close relationship between these two species, at least to the *variabilis* group, and would be a good species pair in which to study the effectiveness of the displays in species identification - behavioral isolation.

The complimentary relationship in distribution between *S. undulatus* (east) and *S. occidentalis* (west) in North America is also suggested by their very similar DAPs. However, *S. graciosus*, which in parts of its range is sympatric with both *S. undulatus* and *S. occidentalis*, not only is suggestive of their close phylo-

genetic relationship, but also provides a basis for a critical study of the significance of displays as an isolating mechanism. These forms are similar in size and the DAP of *S. graciosus* is similar to both of the other two species, i.e., three initial units followed by paired units performed indeterminately. Ferguson (1971, 1973) has studied a sympatric population of *S. undulatus* and *S. graciosus* in Utah and suggests that character displacement in the DAPs may occur in the displays of these two species.

#### Sympatry of species of *Sceloporus* with other iguanid genera.

It is not unusual to observe species of *Sceloporus* and other iguanids in the same habitat. In most examples, the disparity in size would effectively separate these forms, in other habitat preference may keep them apart. For those species of *Sceloporus* which are found closely associated with similar sized species of other iguanid genera in the same habitat, the DAPs are very distinct and probably function well in species identification. Examples of the latter are *S. graciosus* - *Uta stansburiana*, *S. undulatus* - *Holbrookia maculata*, *S. undulatus* - *Anolis carolinensis*, *S. undulatus* - *Urosaurus ornatus*, *S. pyrocephalus* - *Anolis nebulosus*, *S. pyrocephalus* - *Urosaurus bicarinatus*, *S. nelsoni* - *Anolis nebulosus*, *S. nelsoni* - *Urosaurus bicarinatus*, *S. merriami* - *Urosaurus ornatus*, *S. maculosus* - *Uta stansburiana*, *S. couchi* - *Urosaurus ornatus*, *S. teapensis* - *Anolis sericeus*, *S. siniferus* - *Urosaurus bicarinatus*, *S. utiformis* - *Anolis nebulosus*.

The species of *Anolis* usually have a pulsating dewlap as a part of their aggressive display and are smaller in size than the *Sceloporus* they live with in close association (Jenssen, 1971; Greenberg and Noble, 1944). The DAPs of the species of *Holbrookia* (Clarke, 1965) and *Uta* (Carpenter, 1962b, Ferguson, 1971b) differ markedly from associated species of *Sceloporus*. The DAPs of the species of *Urosaurus* (Carpenter and Grubitz, 1960, and unpublished data), a genus with species living sympatrically with a number of species of *Sceloporus*, perform their aggressive displays to a slower cadence than the species of *Sceloporus* with which they come in contact. Milstead (1970) made extensive field observations on a mixed population of *S. merriami* and *Urosaurus ornatus* and observed no interspecific displays between adults of these two species.

#### Display-action-patterns and Size.

When the sizes (snout-vent length) of the species of *Sceloporus* (Table 2) are related to the type of display, certain characteristics appear to be correlated. Those species which exhibit the most pronounced 4-legged pushups are from the small end or small-

ler end of the size spectrum (*jalapae*, *maculosus*, *merriame* and *nelsoni*, *pyrocephalus*, *utiformis*, *siniferus* respectively). With the exception of the *variabilis* and *chysostictus* groups, these forms represent those groups forming one of the two main branches of Smith's (1939) phylogeny for the genus (Fig. 1). Functionally, the more exaggerated 4-legged pushup may be related to body mass-energy expenditure, that is, the larger species would have to exert proportionally more energy in performing fully with all four legs than a smaller species, as proposed by Purdue and Carpenter (1972a), and thus may form the basis for selection for these respective display characteristics.

Table 2. Maximum snout-vent lengths (mm) recorded for the species of *Sceloporus* considered.

144 - clarki
125 - magister
122 - torquatus
121 - olivaceus
119 - spinosus
113 - horridus
112 - edwardtaylori
109 - orcutti
105 - melanorhinus
100 - lundelli
98 - mucronatus
98 - acanthinus
96 - jarrovi
95 - lunaei
91 - dugesii
91 - occidentalis
89 - formosus
81 - asper
80 - cautus
79 - grammicus
78 - variabilis
77 - utiformis
75 - undulatus
74 - cryptus
74 - pyrocephalus
73 - nelsoni
72 - teapensis
72 - ornatus
71 - siniferus
69 - graciosus
65 - scalaris
63 - aeneus

- 62 - *couchi*
- 60 - *chrysostictus*
- 59 - *megalepidurus*
- 59 - *woodi*
- 59 - *merriami*
- 56 - *jalapae*
- 52 - *maculosus*
- 52 - *cozumelae*
- 50 - *parvus*

#### Display-action-patterns and Habitat Niche.

The species of *Sceloporus* live in four general types of habitat niches: arboreal, rocky out-crops and boulders (including crevice dwellers), terrestrial or ground dwellers, and a fourth category including those species that live on or near the ground with nearby cover of shrubs, bushes, logs, fence posts, etc. It is difficult to delimit many species to one particular habitat niche, but when the general partitions are considered certain display characteristics appear related to the type of action in the display. Members of each species group tend to have similar habitat preferences.

Arboreal forms (particularly the *spinosus* and *formosus* groups) have DAPs which are 2-legged, slow cadence, long hold, indeterminate pushup sequences. The saxicolous forms (*torquatus* group, *S. merriami*, *S. couchi*, *S. maculosus*) have more rapid (often jerky) actions in their DAPs. *S. orcutti* (*spinosus* group) which is primarily a rock dweller, has the jerkiest display of its group. Most of the species which are ground dwellers and low shrub dwellers have rapid cadence or jerky DAPs.

Among the species of other sceloporine forms, the species of *Urosaurus* (Carpenter, 1962b) (arboreal shrub and tree dwellers, rarely saxicolous) have indeterminate, long hold, pushup sequences, while the ground dwelling sand lizards (*Callisaurus*, *Cohposaurus*, *Holbrookia*, *Uma*) (Carpenter, 1963, 1967; Clarke, 1965), the horned lizards (*Phrynosoma*) (Lynn, 1965) and the utas (*Uta*) (Carpenter, 1962b; Ferguson, 1971a) have rapid or jerky pushups or head bob sequences.

A lizard displaying in a rapid jerky manner from an arboreal site might be more likely to lose its footing and fall than a lizard performing slowly with long hold in its display. Rapid or jerky performances on the ground, rocky outcrops, boulders, or logs would be less likely to be dislodged by its vigorous actions.

#### Evolution of Display-action-patterns: Speculation.

The performance of pushups, head nods or bobs as a part of the aggressive display is characteristic of all genera of iguanid lizards critically observed (Carpenter, 1967). The presence of this behavior throughout this family strongly suggests it has been present

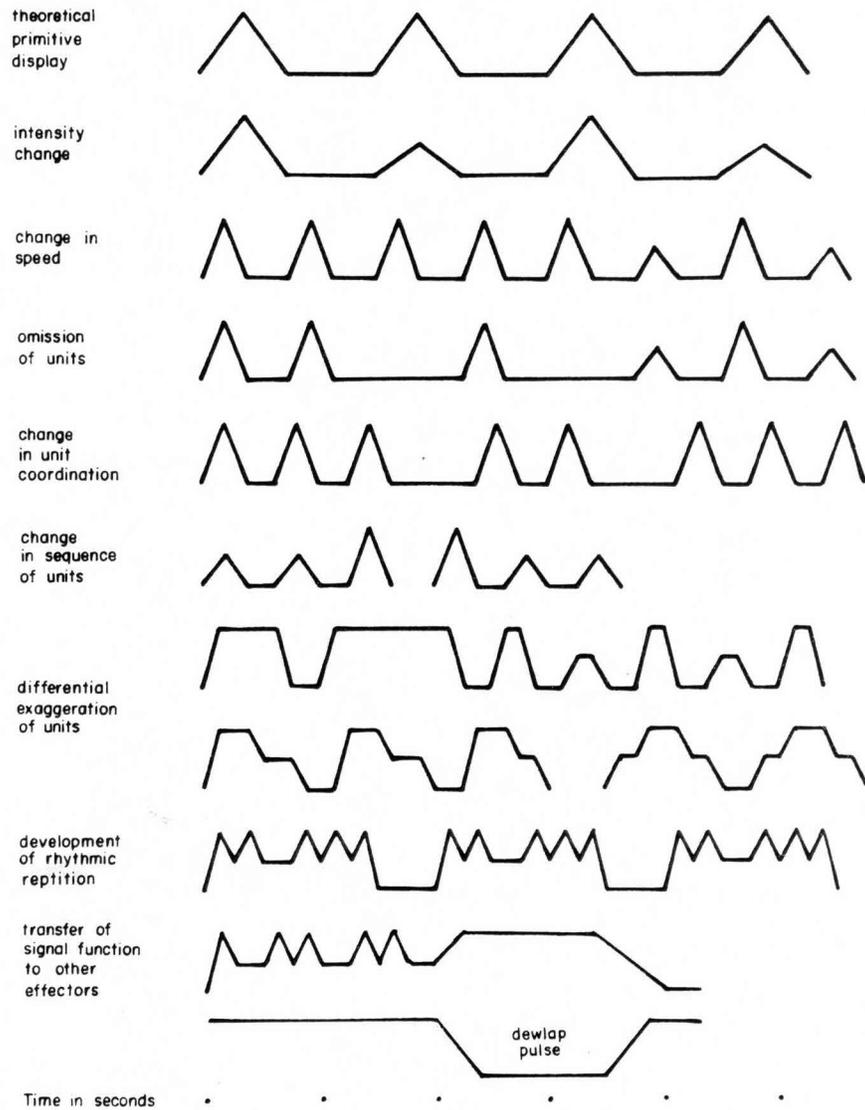


Figure 14. Hypothetical scheme for time-motion coordination changes of simple display movements to product elaborate types of ritualistic displays. See discussion.

as a behavioral trait in its long line of evolution and that extant species represent many modifications and adaptations (supported by the species-specific nature of the display-action-patterns). Since *Sceloporus* is generally accepted as being an advanced genus in the sceloporine line of iguanids (Etheridge, 1964), it follows that the display-action-patterns of its species have probably undergone many modifications from those performed by its primitive ancestors.

Attempts to postulate how display-action-patterns have arisen and produced such a variety of patterns could probably be applied to the entire family as well as to one genus, for one can only speculate on how the primitive ancestral iguanid performed aggressively (pushups, head nods?).

The following hypothetical scheme is based upon the assumption that the primitive form, be it pro-iguanid, or a pro-*Sceloporus* form, performed a simple series of movements. I have adapted a series of coordination changes, suggested by Blest (1961), to postulate how different display-action-patterns might have evolved in the family Iguanidae, and possibly within the genus *Sceloporus* (Fig. 14).

The theoretical primitive display movements, repeated pushups or head nods, are modified by coordination changes in a number of ways. **Intensity change** - successive pushups rise to different amplitudes, i.e., a high amplitude pushup, followed by a low amplitude pushup. **Change in speed** - or cadence so that there are two pushups per second rather than one per second. **Omission of units** - where selection favors the omission of a unit pushup, in effect producing a long pause between successive pushup. **Change in unit coordination** - the sequence of pushup units shifts from three successive units with a pause to two successive units with a pause or vice versa. **Change in sequence of units** - a pattern may become reversed. Differential exaggeration of units, i.e., a medium length pushup, followed by a long hold pushup, followed by short hold pushups, or pushups where the lizard holds at mid-amplitude and at high amplitude during the performance of a unit. **Development of rhythmic repetition** - sequence of units is followed by a short pause and the sequence is repeated, this pattern continuing. **Transfer of signal function to other effectors** - this has not occurred in the species of *Sceloporus* I have observed, but is characteristic of the many species of the iguanid genus *Anolis* where the dewlap pulses in species typical volleys during aggressive displays.

All of the postulated coordination changes produce patterns which simulate to certain degrees those present in the display-action-patterns of species of *Sceloporus*, i.e., Intensity change -

*S. nelsoni*, *S. scalaris*; Change in speed - *S. horridus*, *S. undulatus*; Omission of units - *S. pyrocephalus*; Changes in unit coordination - *S. jalapae*, *S. merriami*; Change in sequence of units - *S. jalapae*; Differential exaggeration of units - *S. dugesii*, *S. formosus*, *S. horridus*, *S. lunelli*, *S. nelsoni*, *S. olivaceus*, *S. woodi*; Rhythmic repetition - *S. aeneus*, *S. dugesii*, *S. jarrovi*, *S. teapensis*, *S. utiformis*, *S. scalaris*.

### Summary

The wide ranging Nearctic iguanid lizard genus *Sceloporus*, with more than 60 species, occupies a great variety of habitats. Species range in size from 50 mm to 144 mm in snout-vent length.

Data were gathered from 1955 through 1972 on the behavior and ecology of 42 species from over the entire range of the genus, in the field and in enclosures at the Animal Behavior Laboratory and the Biological Station of the University of Oklahoma. Displays were recorded on 16 mm motion picture film and analyzed on a Vanguard Motion Analyzer with certain data plotted as display-action-pattern graphs for comparison. Other behaviors recorded and compared included all agonistic activities, courtship and mating.

All species, especially males, exhibit aggression which included challenge and assertion displays, fighting, and chasing. Social dominance and subordination are determined by aggression in enclosures (despotism), which would be represented by territorial in the wild. Patterns of aggression, other than display-action-patterns, are similar in all species. Submissive posture - head, body and tail flattened, legs spread, eye closed, was the same for all species. No significant variation was seen in the above patterns in all of the species of *Sceloporus* observed. The 42 species studied are considered in fifteen subgeneric groups and the eight criteria for comparing aggressive displays are described (including the details of the display-action-patterns), as well as the size, sexual dimorphism in color, habitat niche and social systems for each species. Each display-action-pattern is graphically represented.

The display-action-patterns were compared with the respect to nearest congeners, within subgeneric groups, and between groups, as well as their relationships to size of the species, habitat niche and sympatry within the genus and with other iguanid genera.

Most of the display-action-patterns of the species within groups had similar characteristics indicating intragroup affinities. These affinities were shown in unit sequences, whether determinate or indeterminate, and in cadence. Intergroup comparisons, with some exception, demonstrated group relationships the same as those

served previously from morphological characters. On the basis of display-action-patterns certain new systematic questions are suggested.

Where sympatry occurs for species of *Sceloporus*, display-action-patterns differ significantly and probably act as species isolating mechanisms, with noted exceptions. Either differences in display-action-patterns, species size, or habitat preference were indicated as isolating mechanisms where *Sceloporus* was sympatric with other iguanid genera. In general smaller species of *Sceloporus* exhibited more exaggerated movements in their displays and it was the smaller species which performed four-legged pushups. Possible relationships between habitat niche and type of display were apparent; arboreal forms have slower cadences in their displays in contrast to more rapid cadences and jerky movements for rock and ground dwellers. A hypothetical scheme of time-motion coordination changes is presented to propose how these display-action-patterns may have evolved as species specific ritualistic behaviors.

Significant differences in the display-action-patterns were recorded between all species. Evidence for the species-specific aggressive displays being genetically determined was the consistent pattern of the display-action-pattern within a species, the appearance of these displays in isolation, the lack of alteration of these displays in captivity and after long association with other species, the similarity of displays in closely related forms, and the presence of genetic intermediates in another iguanid genus (*Anolis*).

The criteria for describing and comparing the aggressive displays of all species were: site, position, posture, movement type, parts moved, units of movement, sequence and cadence. The type of movement through time produces the display-action-pattern. The sites used by displaying males were primarily from raised stations with broad visibility. Posturing was little during low intensity displays (assertion displays) and maximum during high intensity challenge displays. Postural changes were similar in all species, though to varying degrees involving dewlap extension, lateral compression of the trunk with some arching of the back. During challenge displays at close range, two males present to each other laterally, heading in opposite direction (face-off). The effect of the posturing and lateral presentation was to show the largest size with the most amount of color, increasing the laterally viewed area by 13 percent. The types of movement were pushups effected by extension and flexion of the legs. The larger species perform primarily front-legged pushups, the smaller species pushup involving all four legs. These pushups vary in amplitude, the length of time held in the up or down position, the speed with which they go up and down, and the patterns of successive pushups in a series

(sequence) through time (cadence). Two general types of sequences were noted; the determinate sequence which has a discreet number of units per sequence and the indeterminate sequence which has a variable number of units per sequence.

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