AN ABSTRACT OF THE THESIS OF

Linda D. Clarke for the Master of Science Degree

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Title: Display Behavior of Leiocephalus, (Iguanidae)

Abstract approved: Robert J Clarke

The taxonomic order of all living things is in a constant state of change due to changes in taxonomic tools. Species-specific behavior patterns, which are innate and stereotyped, are becoming one of the new tools which aid in taxonomic allocation.

The objectives of the study were to identify species-specific push-up patterns for four subspecies of the West Indian iguanid lizard genus, Leiocephalus. Three of these were subspecies of L. carinatus and the fourth form was of a different species, L. schreibersi. A comparison was made of each of the four population-specific patterns by use of cine photography and analysis of single frame projection. Display-action-pattern (DAP) graphs were constructed for all sequences of display. These graphs were analyzed for duration, amplitude, and number of units within a sequence for each of the four subspecies. Comparison of these graphs constituted the bulk of the evidence for arriving at the conclusions drawn.

Display patterns were found to be substantially similar within each population and different between subspecies. Whereas the basic pattern of display of the three subspecies of L. carinatus showed evidence of relationship, the display of L. schreibersi was quite different from any of the others. The latter exhibited three types of head movement display, whereas L. carinatus utilized only one, most of the time. Patterns of the

displays for all of the subspecies are delineated.

Most iguanid lizards utilize either head bobs or push-ups, one or the other, but Leiocephalus incorporates both of these into its display pattern; this is graphically illustrated.

DISPLAY BEHAVIOR OF *LEIOCEPHALUS* (IGUANIDAE)

A Thesis
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Master of Science

by
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INTRODUCTION

Taxonomy and a search for correct phylogenetic relationships among living organisms has brought about various techniques attempting to aid in correct identification. These techniques range from mere physical resemblence to anatomical, morphological, and physiological similarities; no technique has proven entirely adequate. Changes in the taxonomy of various species occur frequently.

In recent years, it has become more and more apparent that species-specific characteristics of behavior patterns can be used to assist in the clarification of taxonomic relationships and to indicate assumed evolutionary lines (Carpenter, 1962a). Previous investigations have shown that display patterns in iguanid lizards are species-specific (Carpenter, 1961, 1962b, 1963; Clarke, 1965; Lynn, 1963).

"A knowledge of variation of displays is biologically significant for at least the following reasons: (1) variation of display intensity of or type within an individual may reflect variation of communicative information and must be considered to fully understand the communication system, (2) display variation between taxa can provide important taxonomic clues for discrimination of similar taxa or for showing their phylogenetic affinity, (3) display variation between populations can provide clues to the potential rate of evolutionary change of displays, (4) correlation of interpopulational display variation with environmental variation can provide important clues to the selective bases for divergence and pave the way for experimental studies of natural selection" (Ferguson, 1977).

Perhaps the first to emphasize that there was some degree of species-specific stereotypy or discontinuity of the variance of particular social displays were Noble and Bradley (1933). Carpenter and Grubitz (1961)

were the first to quantitatively measure species specificty of displays and to originate the display-action-pattern graph, which shows the predictable nature of push-up movements in iguanid lizards. In several papers, beginning in 1962, Carpenter demonstrated that using cinematographic techniques the variation of the timing of the up and down movements in the display could be precisely described and that differences between closely related species existed (Ferguson, 1977).

"A lizard display is typically composed of up and down movements (usually augmented by limb flexion and extension) which are at times interspersed with periods of no amplitude change. Variables which can create different appearing displays are: direction of head movement (constant or changing), relative amplitude of the movement, and the elapsed time between movements. The physical and functional aspects of the displays are referred to by the terms 'display pattern' and 'display type'.

"Display pattern is a descriptive term used to refer to the change in amplitude through time of a lizard's head and dewlap as the lizard performs a head bob display. As a rule, the pattern is reoccurring for a species, which indicates that it is stereotyped.

"Display type is a primary category. It encompasses: (1) the stereotyped head and/or dewlap movement pattern (display pattern), (2) any consistently associated stereotyped movements by other body parts (eg., tail lift), (3) any other postures and movements which less consistently accompany the stereotyped display pattern, and (4) the functional significance." (Jenssen, 1978).

To formally categorize display stereotypy and variability, there are four categories: (1) intra-population stereotypy, those elements of a

display which are consistent for an individual, but are absent or show wide variability between members of a population; (2) intra-individual stereotypy, an element of display which exhibits little intra-individual variability and little inter-individual variability; (3) intra-population variability, any element of display which exhibits much intra-individual variability and little inter-individual variability; and (4) pattern variability, variation in the stereotyped portion of the populations' display sufficient to disrupt that pattern, as produced by (a) a few population members on occasion, or (b) all population members consistently.

The purpose of the present study is to examine intra-specific push-up patterns among four subspecies of the lizard genus Leiocephalus (Iguanidae). The pattern of each species and subspecies is innate and ritualistic for that particular taxon and should show marked species-specific differences among the four.

Distribution

Species of the genus, Leiocephalus, occur on most of the islands of the West Indies, except on Puerto Rico and the Lesser Antilles. One species once apparently occurred on Martinique, but it is thought to be extinct. Today 21 species are recognized in the West Indies, two of which may be extinct. These 21 species are composed of some 82 subspecies, which indicates insular distinctness. There are also introduced populations in the Florida Keys and on peninsular Florida (Schwartz and Thomas, 1975). Fourteen species occur in South America, but Etheridge (IN Peters and Donoso-Barros, 1970) considered the Leiocephalus species there to belong to the genus Ophryoessoides Dumeril.

The four subspecies studied for the present research were collected for animal supply houses and subsequently purchased or were obtained for Dr. Carpenter by a student working on a research project. The lizards

were taken from Bimini, Cayman Brac, Grand Cayman, and Haiti (Fig. 1). Each form is isolated geographically from each of the others.

Description of Forms

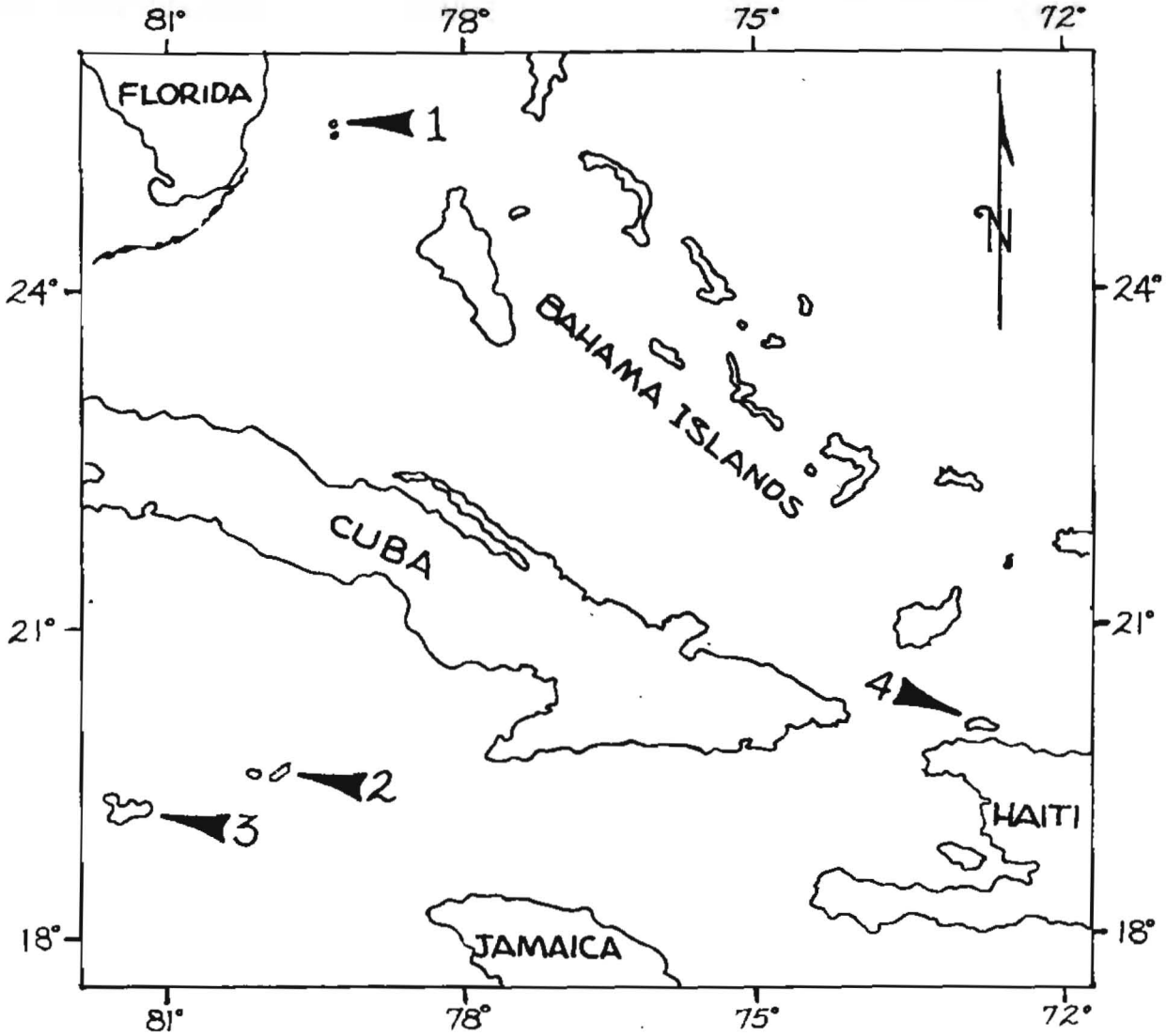
There is great diversity among islands, with some islands having only one form and other islands having several. Most species are not widespread, with only a few subspecies, usually each on a separate island. Since there is no chance for the various subspecies to mate together, there should be divergence in size, color patterns, and behavior, due to isolation and genetic drift. Members of the genus, Leiocephalus, are rather small lizards, ranging around 250-300 mm in total length. Females of the species are usually smaller in size than the males. A striking characteristic of this genus is the tail, which is curled over the back, hence the name "curl-tail lizard" (Evans, 1953). Some forms use the tail more than others in display and natural movement.

Members of the genus, Leiocephalus, are usually brown with darker brown lateral stripes. The head and body may have patches of blue or green. There are variations in the throat patterns, consisting of dots and stripes, which are used in species identification. Generally the females of each species are smaller and duller in color. The underside of the curled tail is marked by dark chevrons on a lighter background.

"The coloration of the adult males appears to be the most conspicuous of the characters separating them (species). Other good characters appear in the number of dorsal scales, the size of the parietals, and the relative proportion of the hind leg to body length." (Cochran, 1941)

Due to differences in the structural formation of each island, varying vegetation, human population density, and predators, the habitat of each subspecies varies. Generally, however, the habitat of Leiocephalus is sandy soil near beaches and leaf litter areas. Some species, though,

Figure 1. Distribution Map of Leiocephalus
1. Bimini Islands
2. Cayman Brac
3. Grand Cayman
4. Ile de la Tortue, Haiti


81°
78°
75°
72°
FLORIDA
1
N
24°
BAHAMA ISLANDS
CUBA
21°
4
2
3
HAITI
18°
JAMAICA

are found farther inland, on rocky areas and around fences. These lizards enjoy the sun and are usually found sunning themselves on top of rocks and limbs.

Leiocephalus carinatus coryi (Schmidt)

L. c. coryi is found in the British West Indies and the Bahama Islands (North Bimini, South Bimini, East Bimini, Easter Cay, Andros, and Berry) (Schwartz and Thomas, 1975). Individuals for the present study were collected on March 30, 1965, on Lyon, Inc., Estate on North Bimini, B.W.I. (Fig. 1). The habitat was carbonate sand with some leaf litter; predominant vegetation was Australian Pine and palm (Vestal, 1965).

This species (Fig. 2) has large keeled and pointed scales on the back that form a slightly raised crest that is more prominent on the dorsal surface of the tail. Coloration is gray to brown, with darker spotting and bands on head and sides. The throat is speckled. Underside of the tail is lighter than the dorsum and has darker brown chevrons. Females are smaller and duller in pattern than males.

L. c. coryi are found in open weeds, coconut stands, beach dunes, and lawns and gardens. They breed during March and April, with the eggs being laid in midsummer. They are diurnal and are usually observed basking. Although they will climb, they are primarily terrestrial. Males curl the tail over the back like a loose watch spring in displays that attract females and drive away other males. This species feeds on any small prey that it can catch (Behler and King, 1979).

Leiocephalus carinatus granti (Rabb)

L. c. granti is found on Cayman Brac and Little Cayman Islands. Individuals utilized in this study were from Cayman Brac (Fig. 1).

The top of the head is solid olive-brown without dark spots; the

Figure 2. Leiocephalus carinatus coryi

Figure 3. Leiocephalus carinatus granti

upper surface has about 12 dim crossbars of alternating brown and greenish-brown from head to sacrum; the lighter, or greenish-brown bars, are set off by a few white-tipped scales. This pattern continues onto the tail as rings in progressive intensity of color. Underside, the chin and throat are diagonally barred with gray and light-yellowish gray; the belly is lighter. Underside of the tail is like the belly near the base and then barred brown and white, grading into vivid black and white distally. "A race of Leiocephalus carinatus distinguishable from all others in its combination of a ringed tail with white and dark brown; a light gray-brown dorsal color, with slightly darker tranverse bars; a relatively light colored head, with little or no dark spotting; and a low number of dorsal crest scales from head to level of vent (mean about 46 in males, 47 in females)" (Rabb, 1957). The tail is curled over the back when in motion or display activity. The male has a definite throat fan, which is functional, and is used during display. Body and tail lengths of males are much longer than those of females. Females are duller in coloration (Fig. 3).

Leiocephalus carinatus varius (Garman)

L. c. varius is found on rocky ground, preferably near a beach area, on Grand Cayman and Swan Islands. Individuals used in this study were collected on Grand Cayman (Fig. 1).

The male is slightly irridescent; the back, top, and sides of head are olive-brown with dark brown, roundish spots; about 12 indistinct crossbands go from neck to base of tail, interspaces are lighter with light tipped scales. Numerous rings are on the tail; the distal half with alternating dark and very light brown rings. They have a light stripe from above the ear to the sacrum along the edge of the back, or the fifth row from the vertebral. A wide, dark band below the light stripe ends

near midbody with two or three branches onto the sides. The throat and chest have alternate brown and light chevrons; the belly is mottled brown, yellow posteriorly. Legs are darkly mottled, and the entire pattern is somewhat blurred. The female is similar in pattern, but the dark crossbands tend to be concentrated on alternate rows of scales and the dark markings on the throat are more pronounced (Fig. 4).

Body of the male is about one-fourth longer than that of the female and has a proportionately longer tail. Males also have a decided and functional throat fan.

This subspecies is found in open, rocky ground, preferably near the beach, but sometimes along stone walls or roads. It spends much time on top of rocks in the sun. The subspecies is omnivorous, feeding on flowers, particularly of the "bay-vine", Ipomocae Pes-Caprae (L) Roth, and on insects and lizards.

L. c. varius does not curl its tail over its back as much as do other carinatus; when in repose the tail is uncoiled. Males actively fight for territory. The young appear around the beginning of August (Grant, 1940).

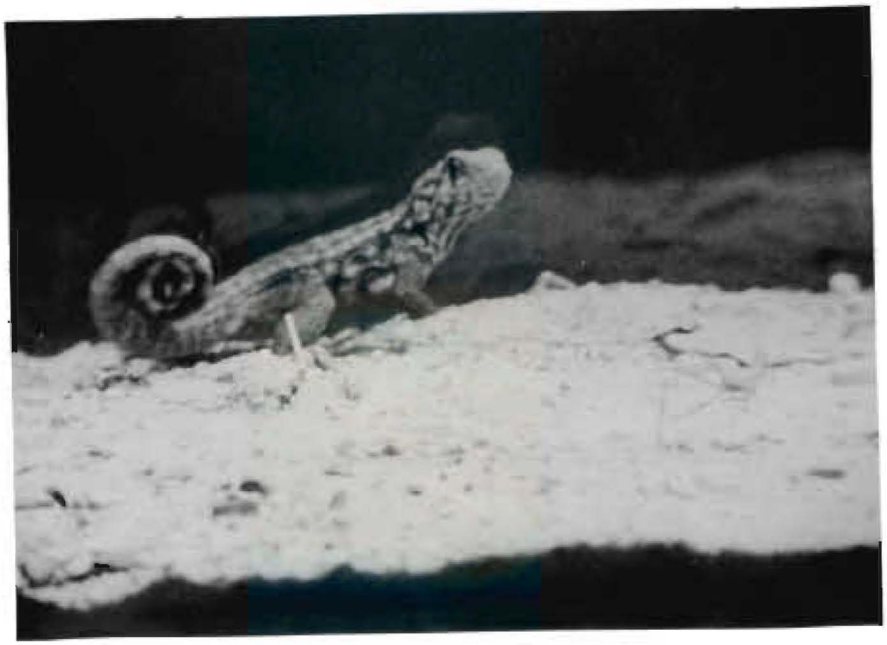
Leiocephalus schreibersi nesomorus (Schwartz)

L. s. nesomorus are found on Palmiste, Ile de la Tortue, Haiti (Fig. 1), and on Hispaniola. Males are found abundantly on sandy beaches, while females and young are found on arid hillsides farther back, as well as the beach area (Schmidt, 1921). Individuals used in this research were reported to have come from "Haiti."

L. schreibersi is strongly sexually dichromatic, but, most distinctly, neither sex has a throat pattern (Schwartz, 1968). Males are generally pale sandy or tan dorsally, and are usually more or less sprinkled dorsally with buffy, yellow, or golden dots. The throat is uniform

Figure 4. Leiocephalus carinatus varius

Figure 5. Leiocephalus schreibersi



grayish-blue to purplish, and may have scattered cear pale blue to green scales on the darker background. There is a series of five lateral orange bars which extend onto the sides of the grayish to pale bluish belly, and which are flecked with pale blue or green scales. Underside of the tail is bright orange, intermixed with pale or brick-red scales. There is at times a turquoise blue patch above the forearm insertion, but in other regions this may be lacking, or even replaced by a bright orange spot. Females are much more drab, are sandier than the males, and lack any orange or green on the sides or back, but have a series of about eight transverse bars or attenuate dumbbell-shaped figures on the dorsum. Females from some localities have golden flecking superimposed upon this basic dorsal pattern. Venter is grayish-white and the throat is basically gray or white, or plain clouded gray (Fig. 5).

The most variable pattern feature is also one of the most striking: the presence in one or both sexes of a black to gray axillary spot. In southern populations, males lack any dark axillary spot, and in southern females this character is variable, and not correlated to either size or geography within the southern population. The black spot is usually absent in southern females. Females are usually smaller than the males (Schwartz, 1968).

Purpose

This research is an analysis of a bobbing movement, known as a "push-up", which is used to display. In Leiocephalus, there seems to be two distinctive types of movements involved in the push-up display: (1) the actual push-up, the flexion of the forelegs, along with their extension, in a repeated up and down pattern, and (2) a head bob, the raising and lowering of the head independent of the push-up. Generally, iguanids utilize one or the other of these movement types in a specific pattern;

Leiocephalus species appear to combine the two. By analyzing the patterns -- taking the number of times the push-up occurs in a particular sequence, the relative amplitude of the individual units, and the duration in time of the sequence, a species-specific pattern should be observed. Elucidation of the patterns for the four subspecies should lead to another means for identification of each of the forms.

Specific objectives of this study are (1) to delineate the general push-up pattern, the number of units within the sequence, and the temporal aspect of the display for each form; (2) to compare the push-up patterns for the four forms of Leiocephalus; and (3) to establish the relationship of the head bob with leg movements in the push-up patterns.

METHODS AND MATERIALS

Most of the data on the push-up patterns of the various Leiocephalus were obtained from films of the different forms, taken by Dr. Robert Clarke, Emporia State University, and Dr. Charles Carpenter, Oklahoma University. L. carinatus coryi, L. c. granti, and L. c. varius were filmed separately by Drs. Clarke and Carpenter during the period 1962-1966. L. schreibersi were purchased from an animal dealer by Dr. Clarke and filmed by him at Emporia in January and February, 1982.

For filming purposes, selected lizards were placed in ten-gallon terraria, which contained sand and rock, to form a more natural environment for display. An infrared light was used to warm the lizards and to generate activity. A 16 mm cine camera was placed on a tripod close to the terraria. Both male and female lizards were marked with paint for individual identification and were photographed in the same terrarium. The size of the terrarium was such that linear movements of the lizards were restricted and they could be kept within camera range, but large enough not to inhibit display activity. This technique also created more push-up displays because the male lizards were not given time to establish dominance and caused more interactions to occur. Once dominance is established in a population, only one male will perform most of the displays (Jenssen, 1978). It was desired to record as many different male displays as possible.

A few of the films were taken with the 16 mm camera stationed on a tripod outside of an 8 X 8 foot metal pen. The pen contained sand, rocks, and grasses to make an environment suitable to the lizards. "A dense habitat is valuable as it shortens line of sight and decreases interactions between dominant and subordinant lizards. Several food and water

dishes are placed on elevated sites around the enclosure to counter the reluctance of subordinate lizards to seek food and water" (Jenssen, 1978). There are disadvantages to this technique, however, as it allows for male dominance over the population and, being a larger area than desired on the camera field, some, perhaps many, displays would be in progress before the camera could be brought to bear.

Displays were permanently recorded by use of two types of cine cameras: (1) a 16 mm Bolex H-16 Reflex, with 100 mm zoom lens, and an 8 mm Bolex H-8 Reflex, with a similar zoom lens. Both of these cameras were set for taking films at 32 frames per second. In 1982, a Sankyo, Model EM-60XL, Super-8 mm camera was also used, which filmed at 24 frames per second. Some of Dr. Carpenter's films were taken with a Keystone cine camera at 16 frames per second. Still photography was accomplished with a Canon A-1 35 mm single lens reflex camera.

Analysis of the motion pictures was accomplished by use of a 16 mm Kodak Analyst single-frame projector and a Kodak Ektagraphic MSF-8 projector, the latter for the super-8 film. Films were projected, frame by frame, on a 11-1/2 X 11-1/2 back-view screen; the vertical displacement of the head of the lizard in each frame was measured and recorded. A plexiglass grid, measured off in 1 mm squares, was placed over the back-view screen, to aid in measuring the amplitude of each movement (Fig. 6). Knowing that the films were recorded at 32 frames per second gave the temporal aspect of the sequence, allowing for accurate time-motion analysis. Information was recorded on a data sheet, each sequence for each lizard for each film was identified on the sheet (Appendix I). The information on the data sheet was later used to make graphs, using number of frames and amplitude of movement as coordinates. The resulting graphs, named display-action-pattern (DAP) graphs by Carpenter (1966), can be

Figure 6. Research equipment.

analyzed by recognizing recurring patterns in sequences of several graphs, identifying each of the units of the sequence by use of an arbitrary number or letter; then measuring each unit in time. The time for each unit of each sequence was recorded, and when a sufficient number of sequences had been recorded, the units' time was averaged (Appendix II), and a composite graph was drawn from these averages, this composite representing the "typical" pattern for that particular subspecies. It was also possible to show the amounts of variation in displays of an individual, among members of the same subspecies, and between subspecies. A comparative analysis of such graphs constitutes the results of this study.

RESULTS AND DISCUSSION

Carpenter (1962a) coined the terms "assertion" and "challenge" to describe a single head-bobbing display pattern in nonanoline iguanid lizards according to the social context in which it appeared. The display can be performed with or without a conspecific present. Under the latter condition, the display pattern shows slight head movement amplitude with few or no modifiers, e.g., throat lowered, body sides compressed. The species-typical display pattern given under these low conflict or motivational situations was labeled the "assertion display". The same display pattern performed under high conflict or motivational situations, e.g., male-male confrontations, is produced with maximum head amplitude movements, i.e., via full extension of the legs, and is accompanied by many modifiers. This form of display is called the "challenge display" (Jenssen, 1978).

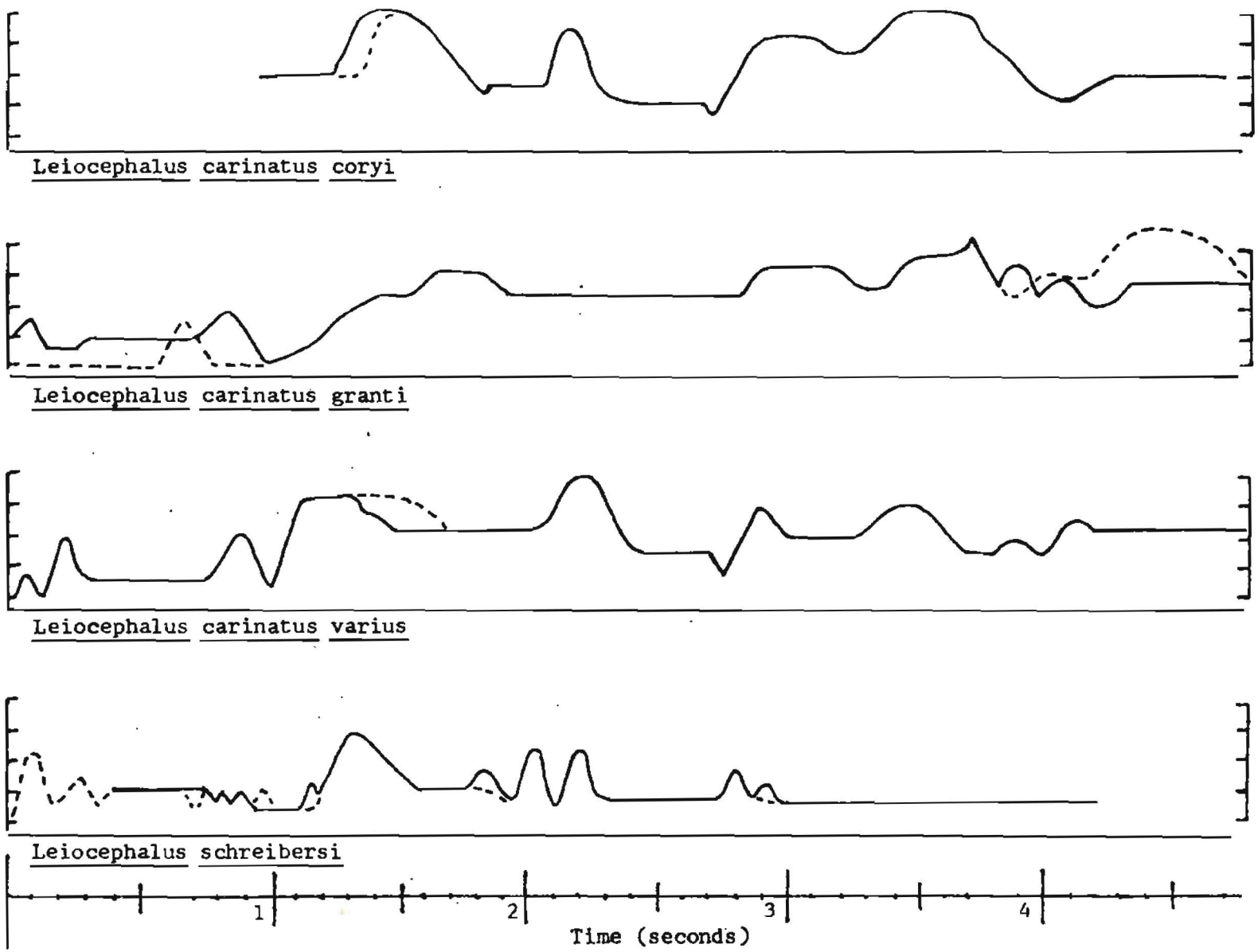
Over 300 DAP graphs were made of the various Leiocephalus forms containing both assertion and challenge display patterns. Of the 300, 93 DAP graphs were chosen and analyzed, as follows: L. carinatus coryi 33, L. c. granti 28, L. c. varius 11, and L. schreibersi 21. Total times were compared for each species and a composite graph of the push-up pattern was made for each (Fig. 7). These composite graphs were compared for each push-up unit in the sequence to find the variation among the four forms.

Leiocephalus carinatus coryi

L. c. coryi had the shortest and least complicated push-up pattern (Fig. 7). Thirty-three sequences were used to derive the pattern, which appeared to be typical.

Of the four forms of Leiocephalus studied, L. c. coryi has the most

Figure 7. Composite DAP graphs for the four Leiocephalus.


Leiocephalus carinatus coryi
Leiocephalus carinatus granti
Leiocephalus carinatus varius
Leiocephalus schreibersi
1
2
3
4
Time (seconds)

widespread distribution. The individuals which were utilized were collected on North Bimini, but the form occurs on a number of the Bahama Islands.

The total time span for the sequence was much shorter, 2.85 seconds, than were the sequences of the other two carinatus observed. A major difference was the length of the pause between movements in the sequence among the three forms. At the top of the extension of the push-up, coryi generally had a short pause before dropping back down to the lower position.

Four subunits made up the total pattern (Fig. 8). Unit 1 consisted of two parts: 1a, a push-up with a pause at the peak of the extension of approximately 0.4 second, a slow drop down to normal position, and 1b, a pause. Unit 2 consisted of a short, high amplitude extension push-up (unit 2a) and another pause (unit 2b). Unit 3 was another extension of high amplitude with a short pause at the top before a slight dropping of the forelegs (unit 3a), followed by a short pause (unit 3b). The push-up of the highest amplitude (unit 4a) was topped with a short pause before a downward fall to normal position. This was followed by another short drop (unit 4b), which ended the typical pattern.

Leiocephalus carinatus granti

L. c. granti, from Cayman Brac, had the longest display among the four subspecies (Fig. 7). The pattern derived from 28 filmed displays by six males and females, consisted of several bobs with short pauses between them, and ending with a series of rapid bobs. The total duration of the display was 4.63 seconds.

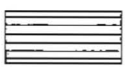
This pattern consisted of eight subunits within the total sequence (Fig. 9). Unit 1 was composed of a quick up and down with a short pause.

Figure 8. Comparative DAP graphs for L. c. coryi and L. schreibersi

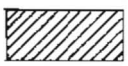
Sub-units are indicated below figure.

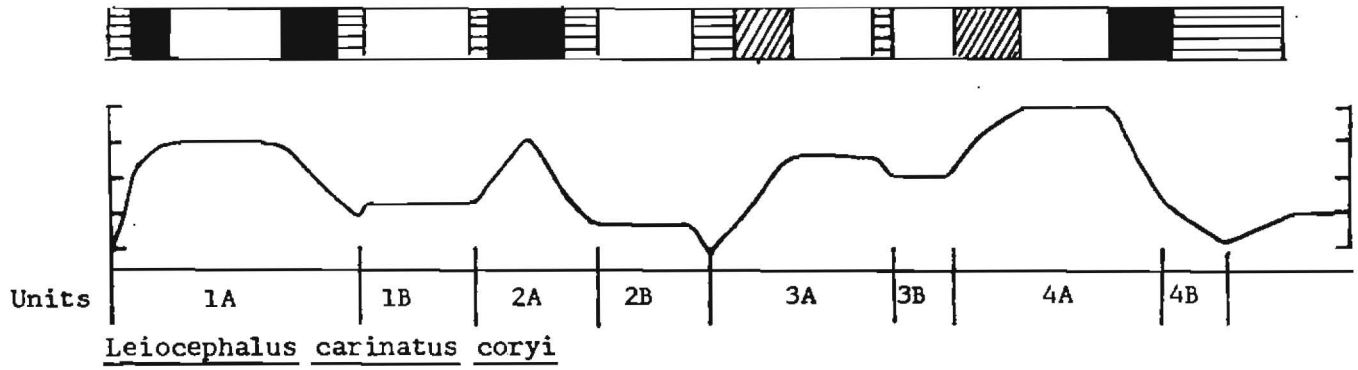
Bar above figure indicates part moved.

Legend:

Head only 

Legs only 

Head and legs 


Units
1A
1B
2A
2B
3A
3B
4A
4B
Leiocephalus carinatus coryi

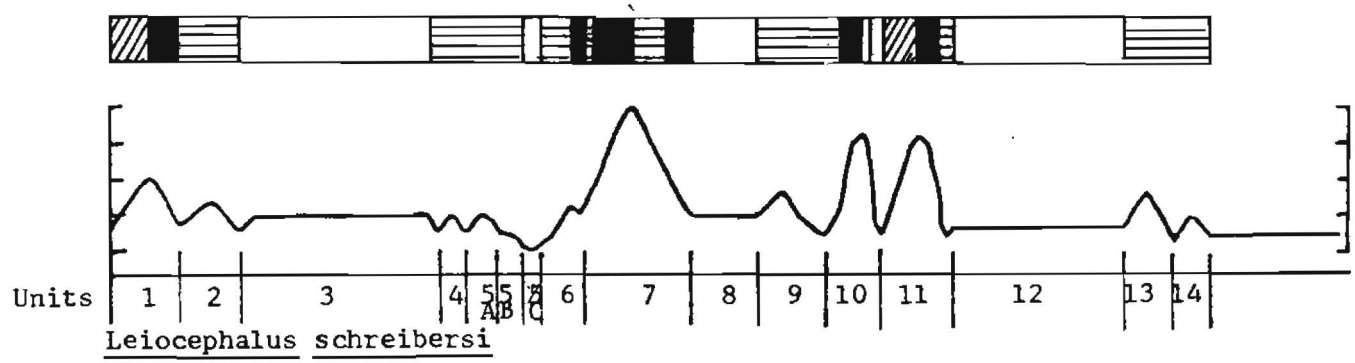

Units
1
2
3
4
5
5AB
5C
6
7
8
9
10
11
12
13
14
Leiocephalus schreibersi

Figure 9. Comparative DAP graphs for L. c. granti and L. c. varius

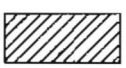
Sub-units are indicated below figure.

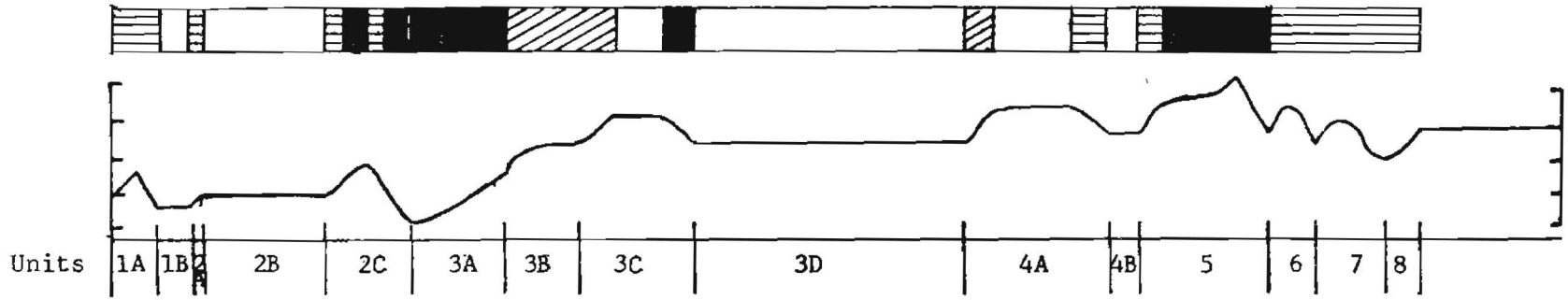
Bar above figure indicates part moved.

Legend:

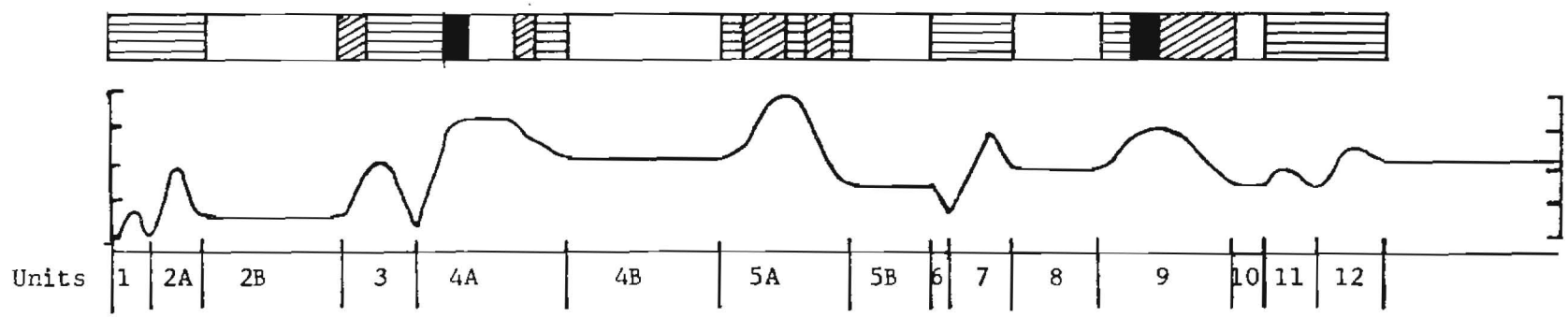
Head only 

Legs only 

Head and legs 



Leiocephalus carinatus granti



Leiocephalus carinatus varius

This was followed by a long pause (unit 2) and a slower, more defined raising and lowering of the head. Unit 3 was a gradual stretching up to the peak of foreleg extension, and a slight drop with a longer pause. Unit 4 was an extension up and down, with a short pause. Unit 5 was a push upward again, approximately of the same duration as unit 4; then back down. Units 6, 7, and 8 were short and very quick head nods, which ended the normal pattern.

There were changes within the pattern caused by individual variation and the purpose of the display. On the whole, the assertion display had the same pattern, but was at a much slower pace and with less amplitude, than was the challenge display. Heightened excitement caused the challenge display to exhibit higher amplitude and greater velocity.

At times a simple head bob was observed. These head bobs seemed to serve as mild to moderate assertion. They consisted of only an up and down movement of the head and neck, with no extension of the forelegs. These assertions varied in number from one to more than six; there was apparently no consistency in their number.

Leiocephalus carinatus varius

L. c. varius are found on Grand Cayman Island, and are most closely related, geographically and by display pattern, to *L. c. granti*. The display pattern was derived from 11 filmed displays from four lizards. As in *granti*, the display pattern consisted of several short bobs with pauses between. The total time for the sequence was 4.20 seconds.

The display pattern was similar to that of the other two *carinatus*, but most similar to *granti*. The primary difference between the patterns of *granti* and *varius* was the length of each subunit: the subunits of *varius* were approximately two-thirds the length of *granti*. Frequency

and amplitude of both were similar (Fig. 7).

Total sequence was made up of 12 subunits (Fig. 9). Unit 1 was a short, fast bob, followed by a short bob of greater amplitude and pause (unit 2). Unit 3 was a slightly longer push-up of the same amplitude as unit 2. Unit 4 consisted of two parts: 4a was a push-up of greater amplitude than before followed by a pause at the top and a downward movement; 4b was a long pause in the down position. Unit 5 also consisted of two parts: 5a, a push-up of the highest amplitude; and a short pause (5b). Unit 6 was a fast drop to a low crouch, followed by a quick, short push-up (unit 7) and a short pause (unit 8). A long push-up (unit 9) was followed by a series of head nods (units 10, 11, 12); thus ending the normal pattern for the sequence.

This pattern was consistent, but had a few variations in it, due to individualism of the lizards. The assertion and challenge displays were similar in pattern, but varied in amplitude or in time of sequence.

Both flexion and extension of the forelimbs (push-up) and head bobs were observed. The head bob consisted of a simple, rapidly accomplished nodding motion and was utilized for mild assertions.

Leiocephalus schreibersi

The display pattern of L. schreibersi, compared to those of carinatus, was very distinctive (Fig. 7). In general, it is a very quick, very short series of push-ups of high amplitude. Total time for a sequence was 2.77 seconds.

L. schreibersi were collected from Haiti, apparently from the Ile de la Tortue, since the specimens key out to that subspecies. These were the only Leiocephalus filmed in 1982. Their coloration and push-up pattern make them quite distinctive from carinatus.

Total sequence was composed of 14 subunits (Fig. 8). Units 1 and 2

were short and very quick push-ups of low amplitude. This was followed by a long pause of approximately 0.5 second (unit 3). Units 4 and 5 were, again, short, very quick push-ups, which dropped to a lower position during units 5b and 5c. Unit 6 had a short, quick push-up, followed by unit 7, a push-up of the highest amplitude and the longest duration. At the bottom of this motion a pause occurred of short duration (unit 9), which was followed by two similar quick, high amplitude push-ups (units 10 and 11). A long pause of 0.5 second occurred (unit 12), followed by two low amplitude, quick head nods that ended the sequence.

It was observed that at the extension of the push-up, as the forelimbs were stretched upward, the neck would pull back toward the shoulders and then extend upward. This motion created the effect of further extension of the body. A rapid head bobbing pattern was also incorporated in the displays which, in the other Leiocephalus, did not seem to be an integral part of the display. This bobbing pattern involved only the head and neck.

The velocity and amplitude of the display sequences were dependent on the type of display pattern, either assertion or challenge. During a challenge display, both males faced each other laterally, extended the legs as far as possible, flattened the sides, and lowered the large dewlap, all of which exaggerated the size of the lizard (Fig. 10). During these face-offs, it was not unusual for one or the other of the males to extend the forelimbs with such force and velocity as to cause the lizard to bounce into the air. Even though these challenge sequences were exaggerated, they still conformed to the general pattern and rhythm, but at an accelerated pace.

Figure 10. Face off between two male Leiocephalus schreibersi.

Comparison

There appeared to be no major differences in the form of the high intensity assertion and challenge when a definite pattern was present in each of the forms of L. carinatus. Leiocephalus schreibersi, however, exhibited three types of display patterns: (1) an unpatterned simple series of head bobs of various number which appeared in mild to moderate assertion; (2) a "jiggle" of the head in which there was a rapid nodding, indicating nervousness or excitement; and (3) a display which had a discernible form, or pattern, to it, given in strong assertion or challenge.

The temporal aspect of units of the three subspecies of L. carinatus indicates similar patterns in the display, but each had a different shape to the movements and a variation in the time period between the movements (Table 1). The two carinatus which are most closely related by geographical location, body pattern, and display pattern are granti and varius. One difference between the two patterns is the time period, or pause period, between the two major units near the center of the display (Fig. 9). The pause period of granti (unit 3d) extends approximately one second, whereas the pause period of varius (unit 4b) is 0.5 second. Also, varius incorporates an extra up and down movement into this period. The other units are about the same for the two. The upward units of granti have short pauses at the top before returning to normal position, which differs from varius, which has more peaked push-ups.

In comparison with the other carinatus, coryi has a much shorter overall push-up pattern and resembles varius more closely than granti (Fig. 7). The peaks and valleys of the pattern are approximately the same as varius in time, but at the top of the peaks there are pauses which are 0.25 second each; and the pauses between the major units are

Table 1. Sub-unit time averages for four *Leiocephalus* in seconds.

Taxon	Sub-units															
	1A	1B	2A	2B	3A	3B	4A	4B								Total
L. c. coryi	.47	.32	.26	.34	.43	.21	.63	.19								2.85
	1A	1B	2A	2B	2C	3A	3B	3C	3D	4A	4B	5	6	7	8	
L. c. granti	.15	.09	.09	.35	.30	.28	.30	.41	.83	.48	.19	.45	.24	.23	.24	4.63
	1	2A	2B	3	4A	4B	5A	5B	6	7	8	9	10	11	12	
L. c. varius	.13	.18	.37	.31	.51	.50	.27	.25	.12	.23	.30	.32	.24	.11	.17	4.01
	1	2	3	4	5A	5B	5C	6	7	8	9	10	11	12	13	14
L. schreibersi	.38	.17	.20	.10	.13	.09	.11	.10	.27	.15	.19	.19	.15	.27	.14	.13	2.77

not as long as the other carinatus. Amplitude of the pattern is greater than either varius or granti. This is due to a higher extension of the forelimbs and neck.

Compared with the other Leiocephalus, schreibersi has a more complex pattern, consisting of short, low amplitude push-ups and intermixed head bobs. There are pauses of about 0.5 second, followed by several active units of varying amplitude. The push-ups of carinatus, on the other hand, are more steady, with pauses and movements of roughly the same time span. General pattern of the display is not similar in timing or appearance to carinatus.

Leiocephalus schreibersi also has a rapid, unpatterned head nodding behavior, attributed to nervousness or stress.

The four subspecies of Leiocephalus studied are from four separate islands, with different ecological conditions (Fig. 1). These forms vary in size, pattern, and sexual dimorphism among the islands. Coloration, sexual dimorphism, scale differences, and presence or lack of a caudal crest have been used for taxonomic descriptions. Another useful adjunct for taxonomic utilization is analysis of stereotyped behavior patterns. Such patterns have been described and their usefulness demonstrated in display of iguanid lizards, the patterns of which appear to be species-typical (Carpenter, 1961, 1962b, 1963; Clarke, 1965; Ferguson, 1977; Lynn, 1963). The present research indicates that the display patterns of Leiocephalus are also distinctive and stereotyped among the forms on separate islands. Further, subspeciation and speciation have evolved because of the separation and because of genetic drift.

Each lizard colonizing a new island represented a certain genetic complement from the original genetic stock. Each island's lizard

population thus originated from a similar but slightly different gene pool and, in time, certain of its characteristics diverged from the parental stock (Carpenter, 1966). Since only one form occurred on each island, interisland differences in the display pattern could not, therefore, be attributed to interspecific competition as a selective agent, and the differences are believed to be the result of genetic drift.

The two subspecies of Leiocephalus carinatus which resemble each other most closely, both by coloration and push-up pattern are varius and granti. The islands on which they are located, Grand Cayman and Cayman Brac, respectively, are only 130 miles apart, but are over 400 miles from Bimini, the locale of coryi, and 500 miles from Haiti, the locality for L. schreibersi (Fig. 1). The nearest land mass to the Cayman Islands is Cuba, 160 miles to the north. Cuba lies between Bimini and the Caymans, and supports a number of Leiocephalus species, including carinatus subspecies (Barbour, 1914; Barbour and Ramsden, 1919; Schwartz and Thomas, 1975). Dispersal to the Caymans may have been from Cuban ancestral stock. Haiti, much more distant from Bimini or the Caymans is less likely to have been a route of dispersal for these forms. Leiocephalus carinatus has a large distributional pattern across the West Indies, indicating that this may be the species from which other species have formed. Speciation on islands is rapid because of separation of the gene pools and is characteristic of insular populations (McCoy, 1969). In addition to the numerous species of Leiocephalus found on so many of the West Indian islands, and Florida, there are some 15 species on the South American mainland, where a closely related iguanid, Tropidurus, is found in a number of species (Peters and Donoso-Barros, 1970) and has invaded the Galapagos Islands where speciation of

the genus rivals the famous "Darwin" finches (Carpenter, 1970). Leiocephalus, has spread among the West Indian islands in a variety of sizes and colorations. Each island group has a number of endemic species, although some species may be widespread. On some of the larger islands several species coexist, but they are separated ecologically. Similarities between subspecies are more evident where the islands are closely located, but, as expected in insular forms, differences on separate islands are apparent. These differences are most likely caused by isolation and genetic drift. "Special behavioral adaptations which were evolved and which are more or less peculiar to the species, are related to the stresses and particular features of its ecological niche" (Carpenter, 1966).

This study has shown that display behavior which is stereotyped can be utilized to distinguish species and subspecies, and could be used as a taxonomic adjunct. Not only can separation of forms be achieved, but also relationships can be shown. Evolution and distributional patterns could be elucidated if sufficient display data were available from all of the islands where Leiocephalus occurs.

SUMMARY

The taxonomic order of all living things is in a constant state of change due to changes in taxonomic tools. Species-specific behavior patterns, which are innate and stereotyped, are becoming new tools which aid in taxonomic allocation.

The objectives of the study were to identify species-specific push-up patterns for four subspecies of the West Indian iguanid lizard genus, Leiocephalus. Three of these were subspecies of L. carinatus and the fourth form was of a different species, L. schreibersi. A comparison was made of each of the four population-specific patterns by use of cine photography and analysis of single frame projection. Display-action-pattern (DAP) graphs were constructed for all sequences of display. These graphs were analyzed for duration, amplitude, and number of units within a sequence for each of the four subspecies. Comparison of these graphs constituted the bulk of evidence for arriving at the conclusions drawn.

Display patterns were found to be substantially similar within each population and different between subspecies. Whereas the basic pattern of display of the three subspecies of L. carinatus showed evidence of relationship, the display of L. schreibersi was quite different from any of the others. The latter exhibited three types of head movement display, whereas L. carinatus utilized only one, most of the time. Patterns of the displays for all of the subspecies are delineated.

Most iguanid lizards utilize either head bobs or push-ups, one or the other, but Leiocephalus incorporates both of these into its display pattern; this is graphically illustrated.

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APPENDIX I

Data Sheet for Recording Movements from Film

Species - Lio. c. granti

3-29-82 2-20-68 ccc-9

3 white spots on back facing left; above another lizard on board							frames per sec.		tape no. C-3	
8	(4)	8.1	7.9	7.9	(24)	8.2	8.5	8.4	8.1	8
7.8	7.5	7.3	7.2	7.1	(3)	7.9	8.1	8.3	8.6	8.8
8.9	9	8.5	7.1	7	(7)	6.9	6.7	6.7	6.8	7.1
7.2	7.1	(16)	7.3	7.5	7.8	7.9	(6)	8.2	(2)	8.4
8.7	8.9	9	(2)	8.8	8.1	8.1	8.1	8.1	8.1	8.1
3.4	(4)	3.5	3.5	3.5	(24)	3.8	4	3.9	3.9	3.9
3.9	3.9	3.9	3.9	3.9	(3)	3.9	3.9	3.9	3.9	3.9
4	4	4	3.3	3.3	(7)	3.3	3.1	3.1	3.2	3.2
3.2	3.2	(16)	3.3	3.4	3.4	3.4	(6)	3.4	(2)	3.6
3.8	4.1	4.1	(2)	4	3.5	3.5	3.5	3.5	3.5	3.5

APPENDIX II

Data Sheet for Averaging Units

Leiocephalus cariuatus varius

TAPE NO.	PATTERN: UNIT NUMBER 1	2A	2B	3	4A	4B	5A	5B	6
1				.22	.47	.54	.31	.28	.10
2				.57	.57	.69	.30	.28	.22
3					.56	.68	.13	.18	.12
4	.13	.15	.33	.72	.72				
5		.15	.46	.28	.68	.36	.28	.28	.09
6					.42	.60	.18	.21	.10
7	.28	.28	.45		.25	.55	.23	.50	.50
8		.25	.25	.42	.85	.30			.12
9					.34	.48	.25	.37	.20
10									.03
11			.36	1.04	1.04	.22	.47	.18	.11
Total	.13	.55	1.85	.92	3.51	4.42	2.15	1.78	1.09
No.	1	3	5	3	7	9	8	7	9
Average	.13	.183	.370	.307	.510	.491	.269	.254	.121