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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

# AN ETHOLOGICAL STUDY OF THE IGUANID LIZARD GENERA CALLISAURUS, COPHOSAURUS, AND HOLBROOKIA

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AN ETHOLOGICAL STUDY OF THE IGUANID LIZARD GENERA

CALLISAURUS, COPHOSAURUS, AND HOLBROOKIA

APPROVED BY

DISSERTATION COMMITTEE

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# AN ETHOLOGICAL STUDY OF THE IGUANID LIZARD GENERA *CALLISAURUS*, *COPHOSAURUS*, AND *HOLBROOKIA*

## CHAPTER I

## INTRODUCTION

Early behavioral information on lizards was relegated to scattered notes, most of which dealt with feeding habits or habitat preference. Only an occasional reference to display or reproductive activity was made. Studies were made by Noble and Teale (1930) and Noble and Bradley (1933) on mating habits of lizards which attracted attention to this group. Evans (1935) reported on the role of hormones in reproductive behavior, and later (Evans, 1938a) on social structure in the genus *Anolis*. Breeding behavior was studied at this time also by Schmidt (1935), and Fitch (1940) conducted a field study on social and reproductive behavior of *Sceloporus*. Thermoregulatory studies of lizards were made by Cowles and Bogert (1944) and territorial behavior studies by Stebbins (1944).

Later, numerous studies were reported which enlarged the scope of the earlier studies of reproductive and thermoregulatory behavior to encompass more groups of lizards, but display and social aspects were largely neglected, except for research conducted by Evans (1951, 1953) and Carpenter (1960; 1961a, b, c; 1962a, b).

During studies on the comparative ecology and ethology of two Oklahoma genera of lizards, Carpenter noted that the iguanid Sceloporus performed a series of body motions, termed "push-ups" or "bobs," with a regular rhythm. He found that the pattern for these push-ups was consistent. Push-ups had been noted in the family Iguanidae for many years, but references to them indicated that no particular pattern was noted. Stejneger's (1893) comments on this behavior of Callisaurus were typical: "Like many other species, it has an odd habit of performing a singular gymnastic exercise, consisting in rapidly dropping and elevating the body with the knees held stiff at right angles to the trunk." It was found that the push-up sequence could be accurately timed in Urosaurus (Carpenter and Grubitz, 1961) and that the pattern and timing of the push-up was not only consistent, but also was species-specific. Hunsaker (1960) described the specific push-ups for the Sceloporus torquatus group of lizards, and Carpenter described push-up display and social behavior in the iguanid genera Urosaurus (Carpenter and Grubitz, 1961), Sceloporus (1961a, 1962a), Uta, Streptosaurus, Urosaurus (1962b), and Dipsosaurus (1961b).

The present study, conducted at the University of Oklahoma, under the direction of Dr. C. C. Carpenter is a continuation and extension of the ethological treatment of genera within the family Iguanidae. The genera Holbrookia and Callisaurus were chosen for study since no organized attempt had been made to describe the various aspects of their behavior.

The objectives of the study were twofold:

1. to describe and compare the display and social behavior of the species of Holbrookia and Callisaurus which occur in the United States.
2. to ascertain if behavioral traits would assist in clarifying the uncertain taxonomic position of the lizard currently known as Holbrookia texana (Troshel).

This investigation was begun in September, 1960, and was concluded in August, 1962. Observations were made at the Animal Behavior Laboratory of the University of Oklahoma, Norman, Oklahoma, except for the summer of 1961, when the study was conducted at the University of Oklahoma Biological Station at Lake Texoma. Observations were also made on numerous field trips during these two years.

Three hundred and seventeen lizards were collected alive for observation. Representatives of every species of the genera Holbrookia and Callisaurus known to occur in the United States were collected. A collecting trip was made from Texas to California in 1960, and additional trips were conducted to Texas in 1961 and 1962. Numerous field trips were made locally in Oklahoma during the two-year period. Specimens were also sent in by interested friends.

## Methods And Materials

During the cold months of the year, lizards were kept indoors at the Animal Behavior Laboratory. Here they were confined in 15 X 10 feet open top enclosures constructed of sheet metal. The floor of the

enclosure was covered with six inches of sand and several large pieces of sandstone were placed in the enclosure to provide hiding places. The enclosures were so placed that sunlight could shine upon the sand most of the day. In addition, heat lamps and sunlamps were used to provide warmth and to supplement the sunlight. Mealworms (Tenebrio larvae) were used for food during the winter months. During the warm part of the year, outdoor enclosures were used, first at the University of Oklahoma Biological Station during the summer of 1961; then at the Animal Behavior Laboratory at Norman during the spring and summer of 1962. The outdoor enclosures were 15 X 15 feet. The sides were made of galvanized sheet metal, three feet wide, one foot of which was buried in the ground. These enclosures were open-topped, except during the last 12 weeks of the study when they were covered with chicken wire. Drinking dishes were provided, and food was obtained by sweeping the weedy fields for insects.

The number and species of lizards kept in the experimental habitats varied according to the plan of observation for any particular time. Those not in this enclosure were kept in cages or in another general enclosure. Observations were made almost daily during the two-year period. The length of time for each observation period was determined by the type of observation being made and by the weather. No observation period was less than one hour, most being of three or four hours. There were numerous days in which the observation period was in excess of ten hours. Observations were recorded and later transcribed, while 35 mm. Kodachromes and 16 mm. motion pictures formed a permanent visual record. A special indoor, glass-fronted enclosure was designed

for use in taking pictures at an angle that could not be accomplished in the outdoor habitats.

All lizards were permanently marked by toe-slipping and were color coded with marks made with fast-drying paint. Males were color marked dorsally in the shoulder region and females were marked dorsally in the pelvic region.

## Taxonomy And Relationships

The lizard genera, Callisaurus, Holbrookia, and Uma comprise a closely associated group which is commonly referred to as "sand lizards." Morphologically, they are quite similar, although modifications to different habitats are apparent.

There has been no recent revision of the genus Callisaurus. Schmidt (1922a) listed three species in the United States, with other species occurring in Mexico. Smith (1946) recognized one species and three subspecies in the United States.

Axtell (1958) revised the genus Holbrookia, and included three species in the genus: H. lacerata, H. maculata, and H. propinqua. The Greater Earless Lizard, known as Holbrookia texana for over a hundred years, was not included by Axtell as one of the species of Holbrookia, although he gave no reason for its exclusion, but referred to it several times as "Callisaurus texanus." My observations of behavior of this lizard, along with other evidence available, supports its separation from both genera, Holbrookia and Callisaurus. Because of this, I prefer to call this lizard Cophosaurus texanus, the name given in the original description by Troschel (1852).

The phylogenetic relationships among genera of the family Iguanidae have been subject to various interpretations. Camp (1923), Mittleman (1942), Smith (1946), and Savage (1958) presented proposals which place the sand lizard group as one of the primitive iguanids or as higher evolutionary stock. The relationship of iguanid genera according to Smith (1946) is given in Fig. 1.

Axtell (1958) illustrated the phylogenetic relationships within the sand lizard group. My concept agrees except for giving generic status to Cophosaurus (Fig. 2).

Holbrookia lacerata is made up of two subspecies, which differ only in minor features of the markings. These lizards have an adult snout-vent length of 60 mm.; the tail and body are about the same length. The body is squat and the legs are only moderately long. Ground color is light brownish gray with four series of dark roughly crescent-shaped markings along the body and upper surface of the tail. Laterally, there are three or four small dark oblique marks on the body. The under surface of the tail bears a series of six or seven black dots, linearly arranged, fading as they progress distally. The other species of Holbrookia do not possess these spots. Like the other members of the genus, as well as Cophosaurus, the tympanum is not exposed. The species is found from west-central Texas to coastal Texas in the vicinity of Corpus Christi and southward into northeastern Mexico (Fig. 3). It avoids aeolian sands and is found most often in Caliche soils of the Edwards Plateau and in cultivated fields and other flat areas to the southeast. H. lacerata occurs where vegetative cover is scant or lacking. Descriptions of the species were given by Cope (1900), Schmidt

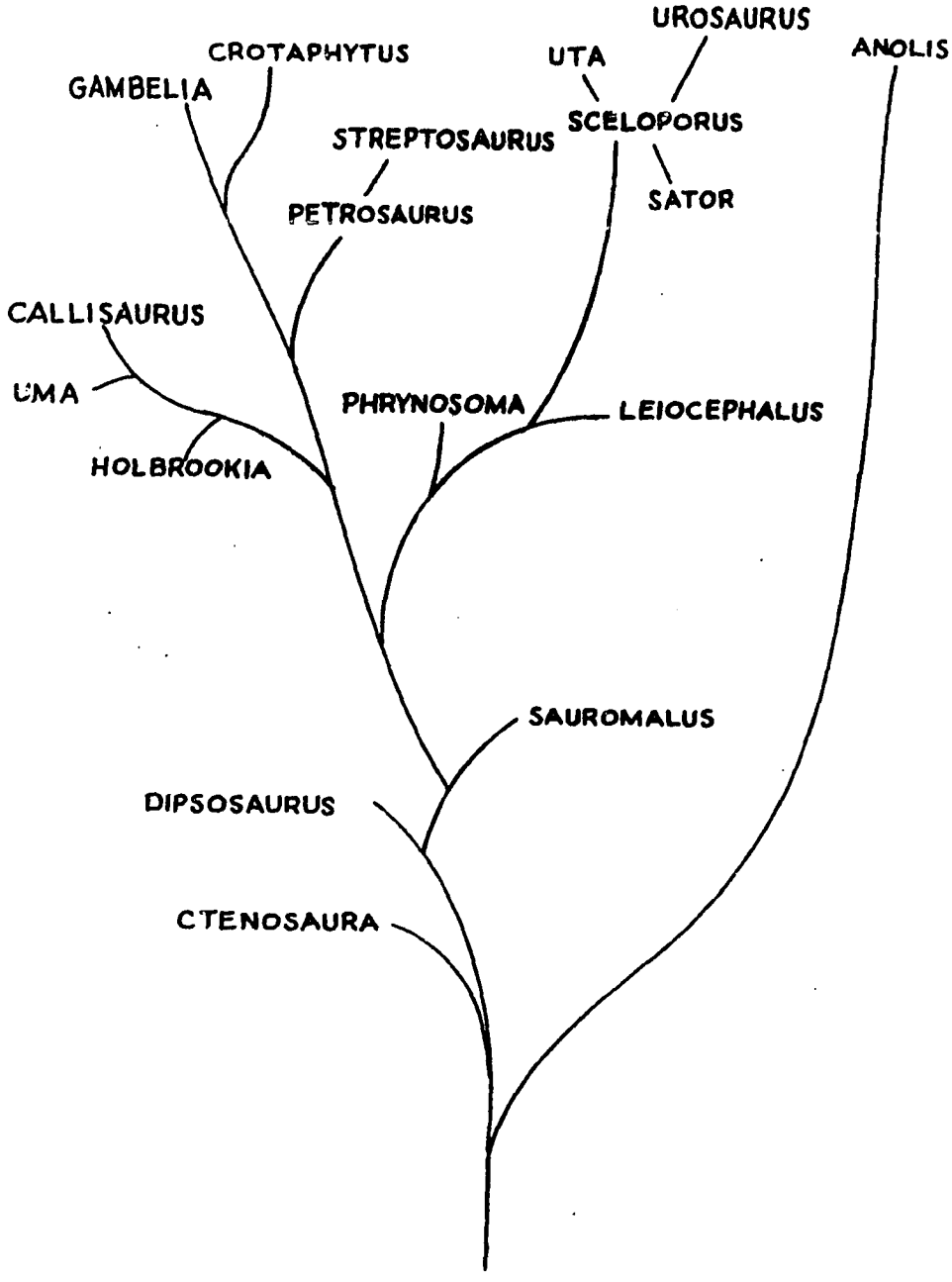



Fig. 1. Phylogenetic relationships of iguanid lizard genera occurring in the United States according to Smith (1946).

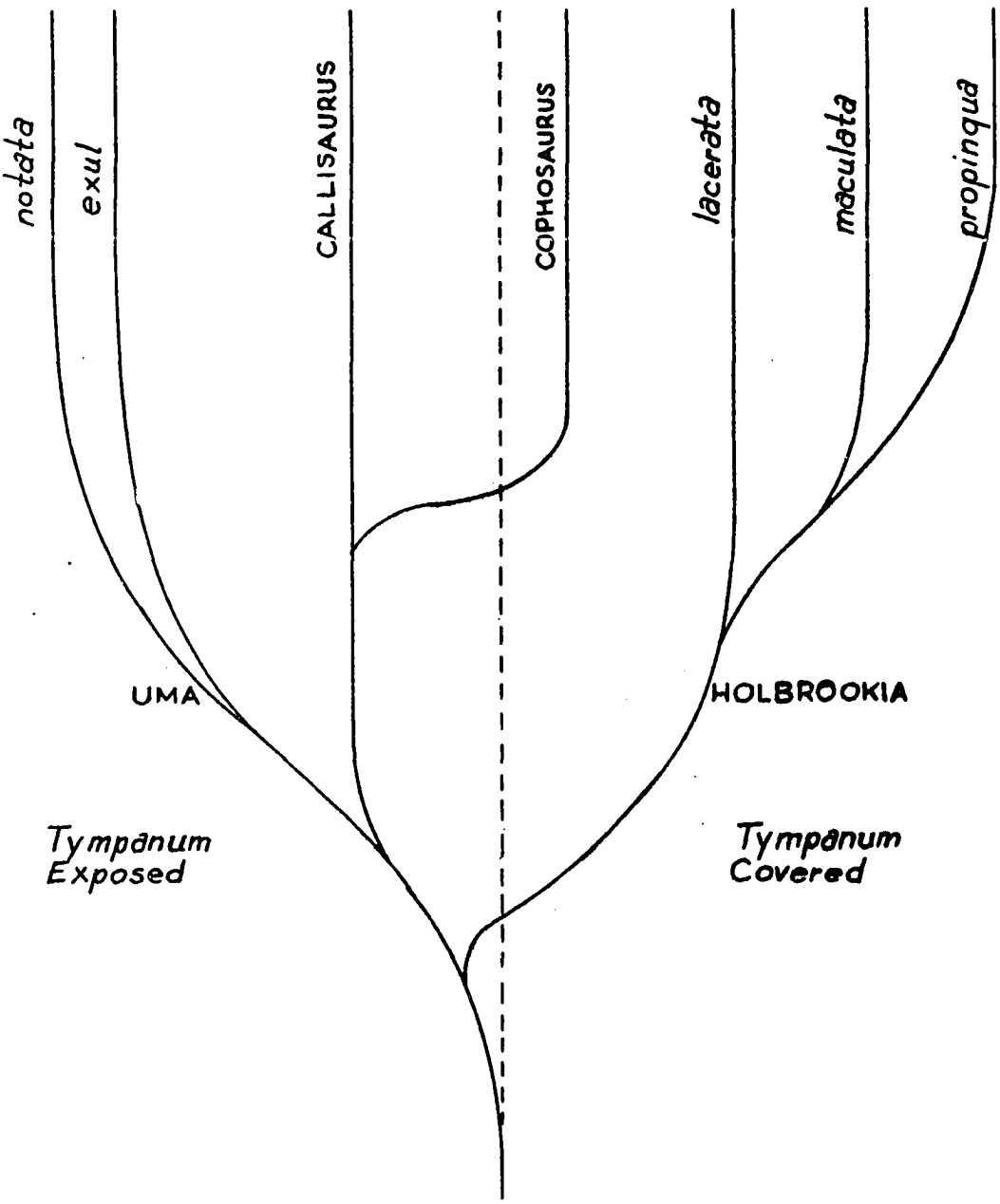



Fig. 2. Phylogenetic relationships within the sand lizard group of iguanid lizards, modified from Axtell (1958). Cophosaurus is given generic recognition. Axtell indicated it as a species, texanus, of Callisaurus.

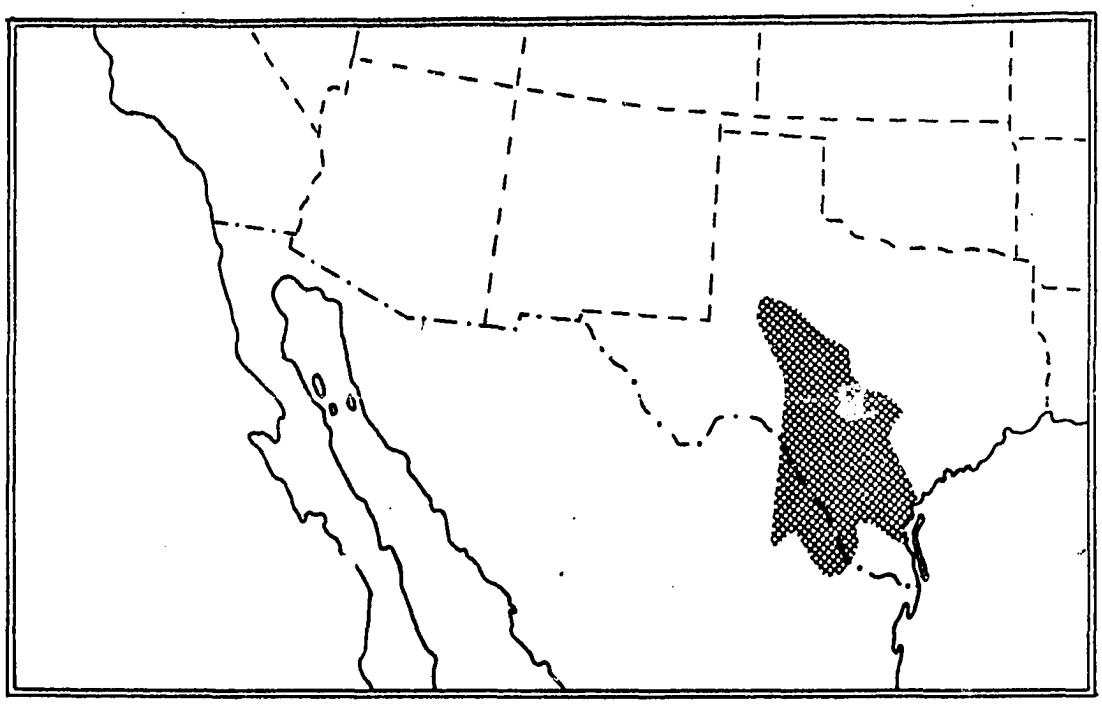


Fig. 3. Geographic distribution of Holbrookia lacerata.

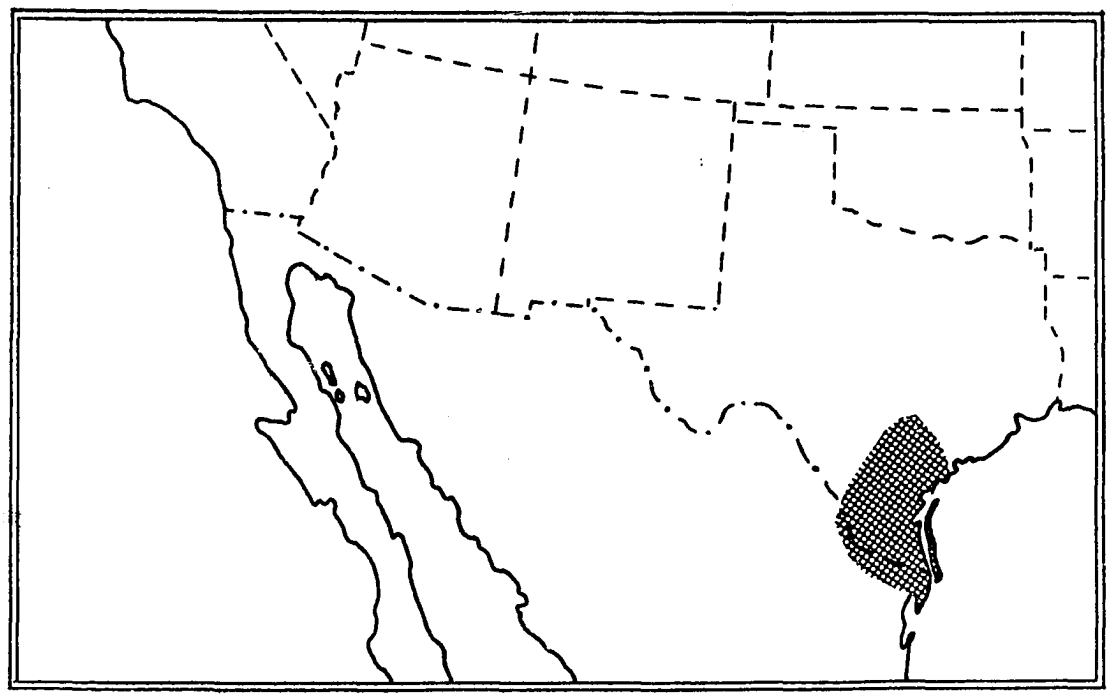


Fig. 4. Geographic distribution of Holbrookia propinqua.

(1922b), and Axtell (1956). The last described the subspecies and delineated the range and ecological conditions.

Holbrookia propinqua differs from the other species of the genus in possessing keeled scales. The body is more elongate and the hind legs longer in proportion to the body than in the previous species. The tail is longer than the snout-vent length, also. These are small lizards, the snout-vent length averages from 55 to 60 mm. The color varies from olive gray to brownish gray, and the pattern usually consists of numerous yellowish spots, although a pattern of paired dark dorsal blotches may be evident. The oblique lateral black bars are more distinct in males and are two or three in number. They lack a surrounding blue tint and are placed about midway along the side of the body, but a little closer to the axilla than the groin. This placement is the same in the other species of Holbrookia.

H. propinqua is confined to the southern portion of Texas and adjacent Mexico (Fig. 4). Ecologically, it is restricted to aeolian sand dunes, where it is found in large numbers in and around the low. scattered vegetative cover. Descriptions of the species, ranges, and ecology were given by Smith (1946), Axtell and Wassermann (1953) and Axtell (1958).

Holbrookia maculata is a widespread species composed of eleven forms, seven of which occur within the borders of the United States; the others in Mexico (Axtell, 1958). All of the forms are small and squat, the snout-vent length of adults averaging between 55 and 60 mm. The tail is about the same length as the body. The pattern is quite similar to that of H. lacerata, but there are no subcaudal black dots. The

oblique lateral bars are more pronounced and are usually two in number, occasionally three. These bars are edged with a bluish tint and are more obvious on the males than on the females. Some variation exists in color and pattern among the subspecies, involving in most cases the suffusion of, or lack of, yellowish spotting in the dorsal pattern. In the White Sands Earless Lizard, H. m. ruthveni, the ground color is white and the pattern is almost nonexistent, except when the lizard is cold. The black lateral bars are quite obvious, however.

H. maculata ranges from Kansas and Nebraska in the northeast to Texas in the southeast and westward into Wyoming and Arizona and northern Mexico (Fig. 5). This is a terrestrial lizard, seldom climbing onto rocks and other raised objects in its environment, although Axtell (1958) states that both H. m. elegans and H. m. thermophila " . . . show a proclivity for perching on isolated rocks . . . " and that this may be characteristic of these forms. The soil types preferred vary from loose dune sands, through cultivated fields, eroded clay soils, to gravelly, flat desert. The soil must be friable enough to allow these lizards to bury themselves and the vegetation must be scant. Descriptions were given by Schmidt (1922b), and ecology and range, as well as descriptions, by Smith (1946) and Axtell (1958).

Cophosaurus texanus is a larger species, the snout-vent length averages from 65 to 70 mm.; the tail is somewhat flattened and longer than the body length by up to one-third. The tympanum is not exposed. Dorsal color is blue-gray to gray with a series of paired, small, dark, rounded spots along either side of the mid-dorsal line, these spots joining and becoming more prominent on the dorsal surface of the tail.

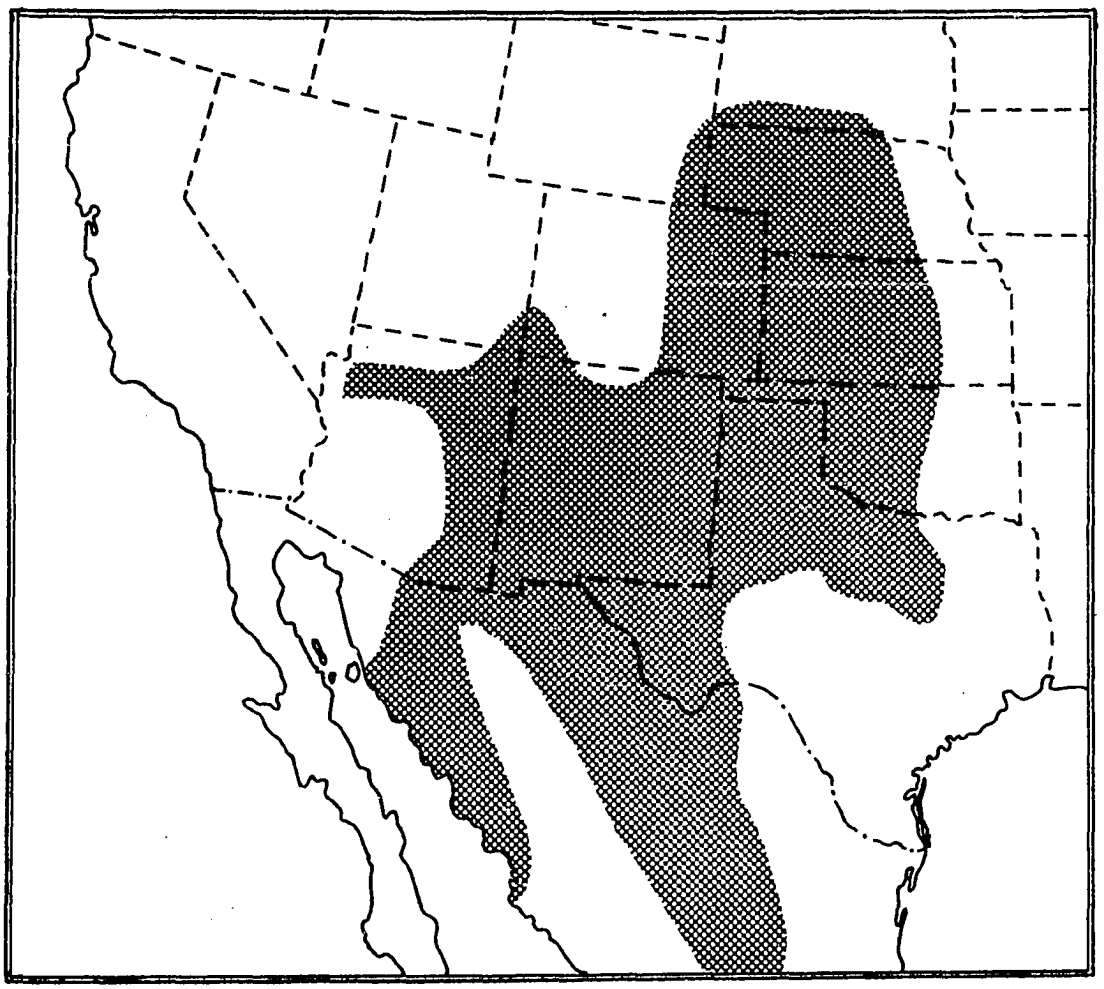


Fig. 5. Geographic distribution of Holbrookia maculata.

The undersurface of the tail has a series of black bands which join with the dorsal spots; the remainder of the undersurface of the tail is white. A pair of ventrolateral dark bars on each side is present, vividly present in males, which extend upward from the lateral fold just anterior to the inguinal region onto the back, arching forward and disappearing in the mid-dorsal region. Males are also highly colored, with a reticulate pattern of spots of orange and blue anterior to the dorsolateral bars. In addition, a large patch of blue or blue-green adorns the ventral region, surrounding the base of the bars and often extending from the inguinal region to the axilla. A black stripe is present on the posterior of the thigh. Three subspecies were described by Peters (1951), who gave ranges and descriptions of patterns and color, as well as certain features of the life history and ecology.

This species inhabits arid desert flats and low hills where " . . . They are more or less restricted to rocky areas" (Smith, 1946). This preference for rocky areas was noted by Jameson and Flury (1949), Ortenburger and Ortenburger (1926), and Peters (1951). They occur generally on gravelly soils where vegetation is open. Cophosaurus ranges from central Texas westward to central Arizona and southward into Mexico (Fig. 6).

Callisaurus draconoides, the Gridiron-tailed Lizard, has a snout-vent length from 70-75 mm. in females to a maximum 93 mm. in males. The tail is about 10 per cent longer than the body length. The hind legs are extremely long, averaging 93 per cent of the length (Smith, 1946). Unlike the preceding species, the body is slender, the lizard having the appearance of being emaciated. In coloration, it is quite like

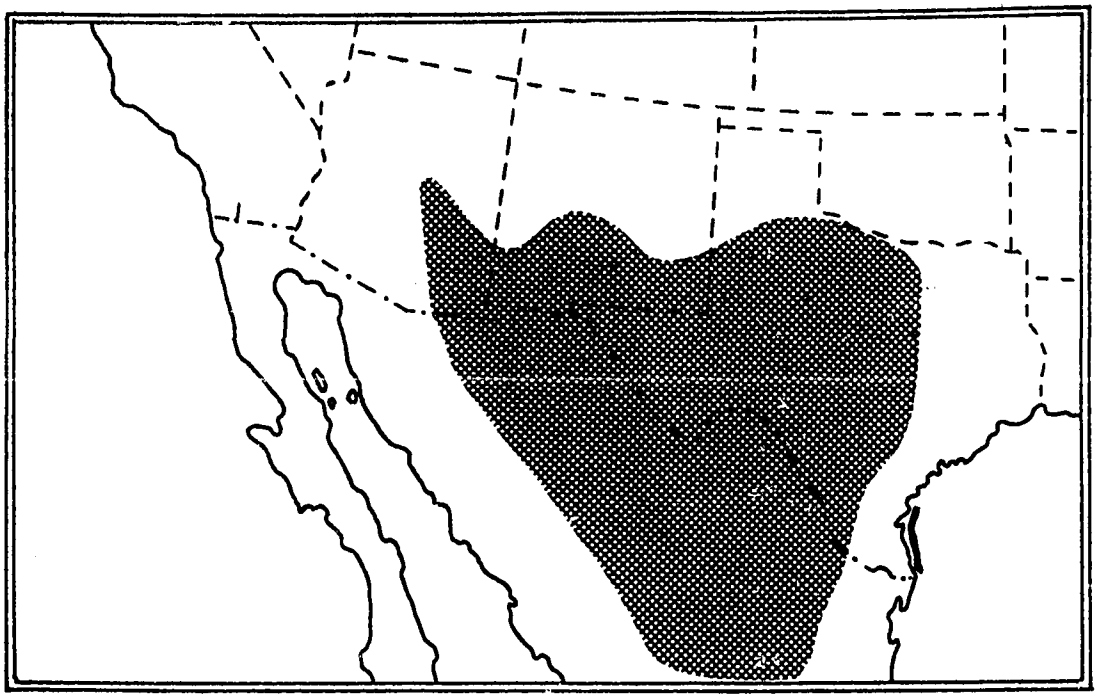


Fig. 6. Geographic distribution of Cophosaurus texanus.

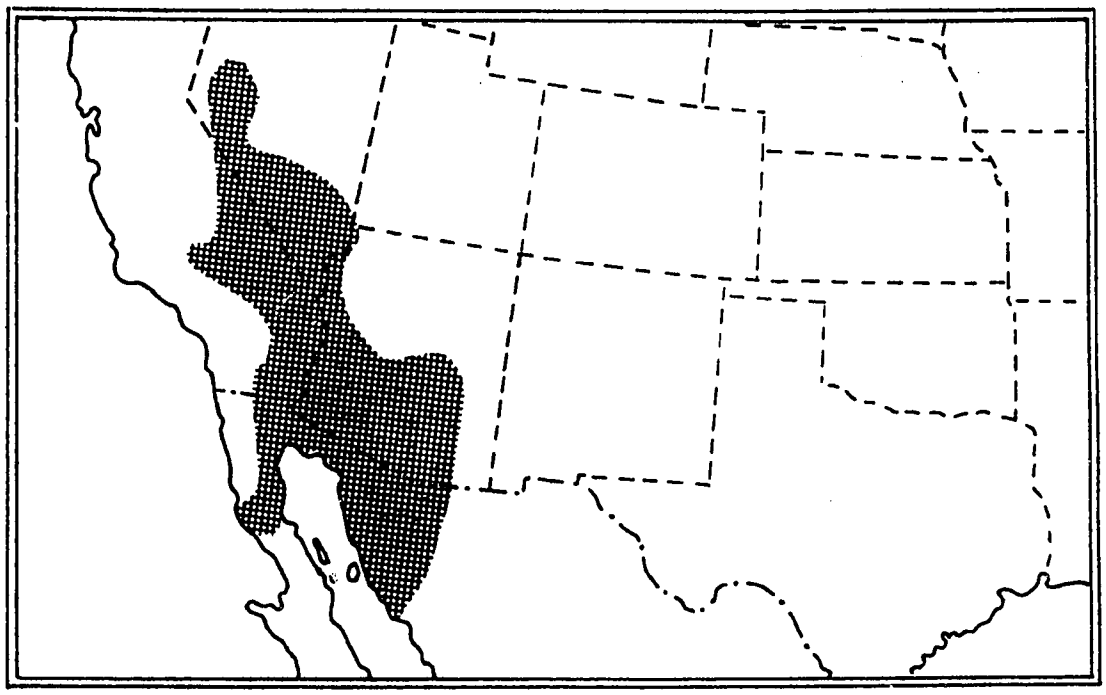


Fig. 7. Geographic distribution of Callisaurus draconoides.

Cophosaurus, but somewhat lighter in ground color. There are seven or eight black spots on the underside of the tail, which join with the dorsal caudal markings to form bands around the tail. These bands are separated by about the width of the band. Two black dorso-lateral bars are present, more prominent in the male, which are placed obliquely a short distance posterior to the axilla. These bars extend onto the ventral surface, where they are expanded and extend almost to the vent. Large blue, navy blue, or greenish patches surround these ventral bars in the males and extend from axilla to groin. In Callisaurus there is an obvious ear opening.

Callisaurus is an inhabitant of flat gravelly desert, foothill washes, and sandy areas. It occurs among low scattered shrubs and does not inhabit rocky areas. The genus occurs in the United States in Nevada, Arizona, and California, and also in northwestern Mexico (Fig. 7). Van Denburgh (1922) described the species of Callisaurus in the United States and Schmidt (1922a) those in Mexico. Tevis (1944) gave habits and ecology. Ecological data were also given by Klauber (1939), Richardson (1915), and Mosauer (1936).

# CHAPTER II

## DISPLAY

Stereotyped display which shows to best advantage certain colored areas of males of the family Iguanidae has been noted by observers of several genera (Evans, 1938b; Fitch, 1940, 1956a; Noble and Bradley, 1933; Oliver, 1948; and Carpenter, 1961a, b; 1962a, b). Display by the male is used to advertise himself to other lizards, to declare territorial rights, to challenge the presence of another lizard, and to court a female. Courting consists of the male approaching the female with head lowered and rapidly nodding. The aggressive or assertive display differs from courtship in that the dewlap is expanded, the sides of the body are compressed, and the lizard presents himself laterally toward his opponent. Behavioral patterns of display are much alike in the various genera and vary only in detail. Callisaurus, Cophosaurus, and Holbrookia conform to the general iguanid pattern.

### Alert Posture

A lizard that is active moves about his habitat from one lookout station to another maintaining an alert attitude. In the "lookout" or "alert" posture the lizard assumes a position with the head held up and the forepart of the body elevated by extension of the forelegs;

the hindquarters rest upon the substrate. From this position the lizard attentively regards his surroundings. Callisaurus and Holbrookia most frequently use flat substrate or hillocks as lookout points, sometimes placing the forefeet upon a small pebble or other raised object. Cophosaurus, however, regularly seeks lookout stations on rocks or other large raised objects and, although they may crawl upon a log or stump, they do not ascend the trunk of an upright tree. The alert posture is alike in Cophosaurus and Holbrookia, but differs slightly in Callisaurus, which has a swaybacked appearance (Fig. 8). Stejneger (1893) called attention to this peculiar stance, "The attitude of this lizard when at rest differs from that of most others in that the knees and elbows stand out at right angles from the body and are elevated to such a degree that they nearly reach the plane of the back."

In the alert posture the signal coloration of the male is not obvious, but in both challenge and assertion marked changes in posture occur which enlarge the profile of the lizard and emphasize the areas of gular and ventrolateral color.

## Challenge Display

Carpenter (1962a) presented eight categories for analyzing display behavior of iguanid lizards. These are utilized below for describing and comparing the species in the present study. These descriptions will be of the challenge display, which is of high intensity.

Site. Holbrookia and Callisaurus performed challenge display on flat ground almost without exception, but Cophosaurus frequently displayed from a rock or other raised object. The most intense challenge

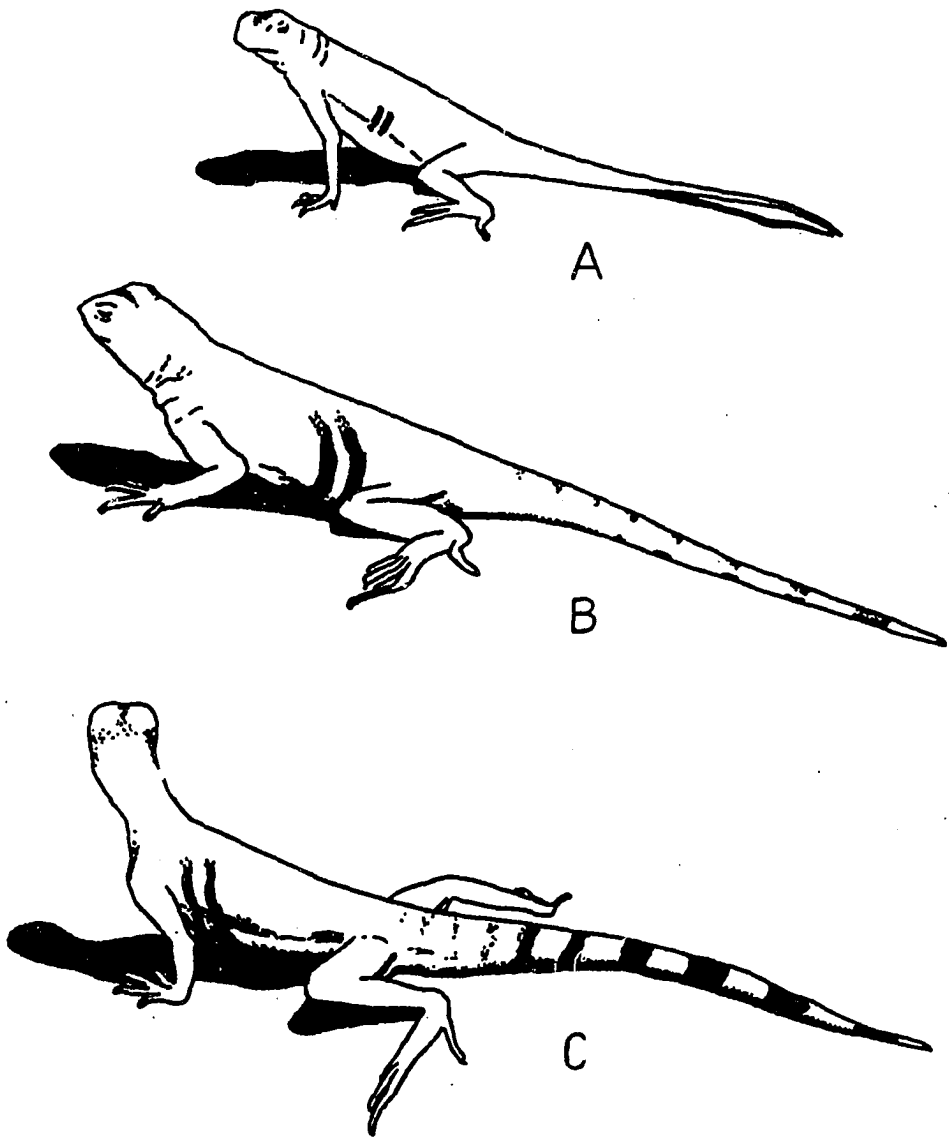



Fig. 8. Difference in attitude of genera in alert posture: A. Holbrookia, B. Cophosaurus, C. Callisaurus.

of Cophosaurus was performed upon flat ground after preliminary assertion and challenge from a raised position. In almost every case the challenge of each species was performed in the same plane as the lizard challenged.

Position. Orientation of the long axis of the body in each species was parallel to the surface of the substrate. In respect to the recipient of the challenge, the orientation of the body was lateral. Two males would present laterally to one another in what is known as the "face off," each heading in a direction opposite his opponent (Fig. 9). This orientation prevailed, for, if one of the pair turned to head in the opposite direction, so did the other lizard. The vertical plane of the body of each lizard was tilted toward his opponent, this being most exaggerated in Callisaurus.

Posture. Lateral compression of the body was performed in each form. This caused exaggeration of the silhouette of the individual, giving the appearance of a large increase in size. In addition, the black bars on the side were brought into prominence and the large blue or green ventral colored areas of Callisaurus and Cophosaurus were exposed. These areas of color were not present in Holbrookia. A very definite large dewlap was expanded in Callisaurus and Cophosaurus, which was colored with an orange-pink suffusion. A small dewlap was apparent in Holbrookia, but it did not approach the relative size of the dewlap in the other genera, nor was it colored.

In each genus, the lizard elevated with the shoulders and hips in almost the same horizontal plane. The legs were flexed slightly, the back was arched, the head lowered, and the tail held out stiffly behind or on the ground, with the tip twitching from side to side. The head

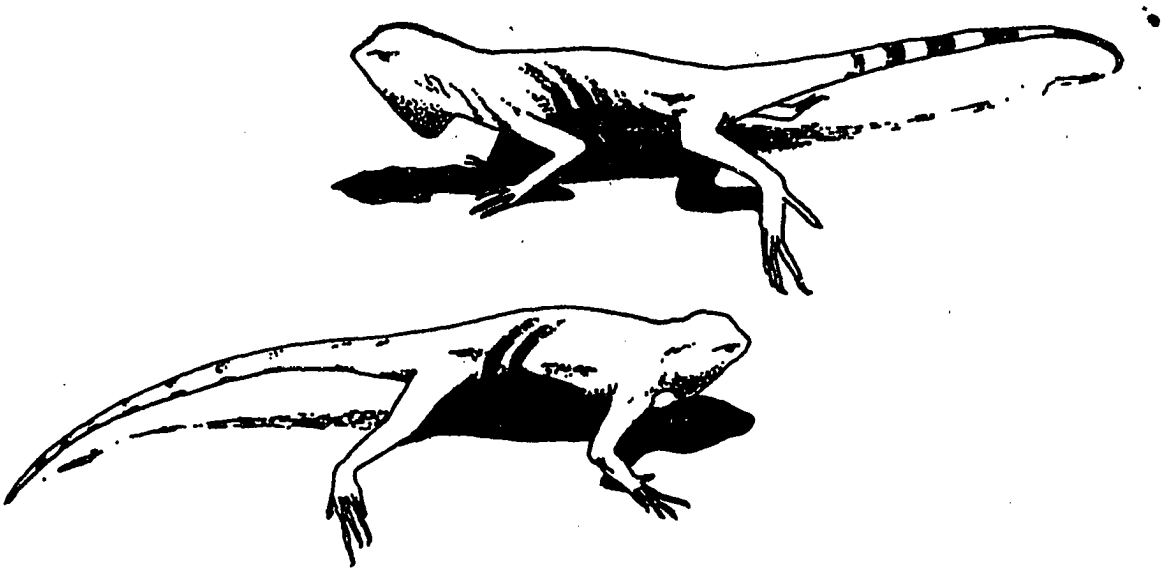


Fig. 9. Face off attitude assumed when two males challenge in lateral presentation. Upper lizard, Callisaurus; lower, Cophosaurus.

was turned in slightly toward the adversary. This position was maintained stiffly, except when the lizard was performing push-ups. Even then, only the front legs were moved, the rest of the lizard maintaining its rigidity.

Movement type and parts moved. In challenge display, the lizard is raised with legs slightly flexed. From this position the forepart of the body is lowered and raised by flexion and extension of the forelegs. The body is lowered until it almost touches the substrate and then raised. This is repeated a specific number of times for each species. Push-ups begin from a crouched position or from a highly extended posture. During the push-up all of the body remained rigidly motionless, except for the movement caused by the action of the forelegs.

Hunsaker (1960), Carpenter (1961a, b; 1962b), and Carpenter and Grubitz (1961) described push-ups for iguanid lizard genera. From their observations it is obvious that patterns exist in push-ups which can be described as species-specific.

A 16 mm. Bolex reflex motion picture camera with a 100 mm. telephoto lens was used to record the push-ups of the lizards studied. Each sequence was exposed at 16 frames per second. When the film was run through a large film editor, the amplitude of the push-up could be measured directly, and the attitude of the lizard in each frame noted. These notations were transferred onto a strip of paper placed over a grid representing the frames of the film. Thus, when an entire sequence of a push-up was recorded and points representing the position of the lizard in each frame placed on the paper strip, adjacent points could be joined with a straight line, creating a diagram of the push-up. A scale was

developed which could be used to indicate tenths of a second on the paper strip. From inspection of the strip, the units, sequence, and cadence of the movements could be ascertained.

Motion pictures were made of numerous push-ups of each of the species studied. These were made in outdoor enclosures and in specially lighted indoor terraria, where, in the latter, it was possible to photograph the lizard on a horizontal plane. The following information is based upon an analysis of these pictures by the method described above. Display-action-pattern-graphs (DAP-graphs) for each species are illustrated in Fig. 10.

It is apparent that the push-ups of the three species of Holbrookia are quite similar. It is also apparent the push-up patterns of Holbrookia, Cophosaurus, and Callisaurus differ distinctly.

Units of movement. Carpenter (1962a) defines the unit of movement as "A distinct and measureable change in position or posture, of one or more movement types, which may or may not be repeated." He considered the unit to begin with a lowering of the body and end with the return of the body to the position from which it started, after having performed one or more dips with no obvious pause between the dips. In the present study it was found that a different concept of the unit could be utilized more advantageously. Thus, the "unit" referred to hereafter will begin with a movement of the lizard's body upward and end with the body in a lowered position. The unit may consist of a single raising and lowering of the body or may be composed of a series of elevations and dips of various heights, the movements of which follow one another without a prolonged pause. At the end of the movements of

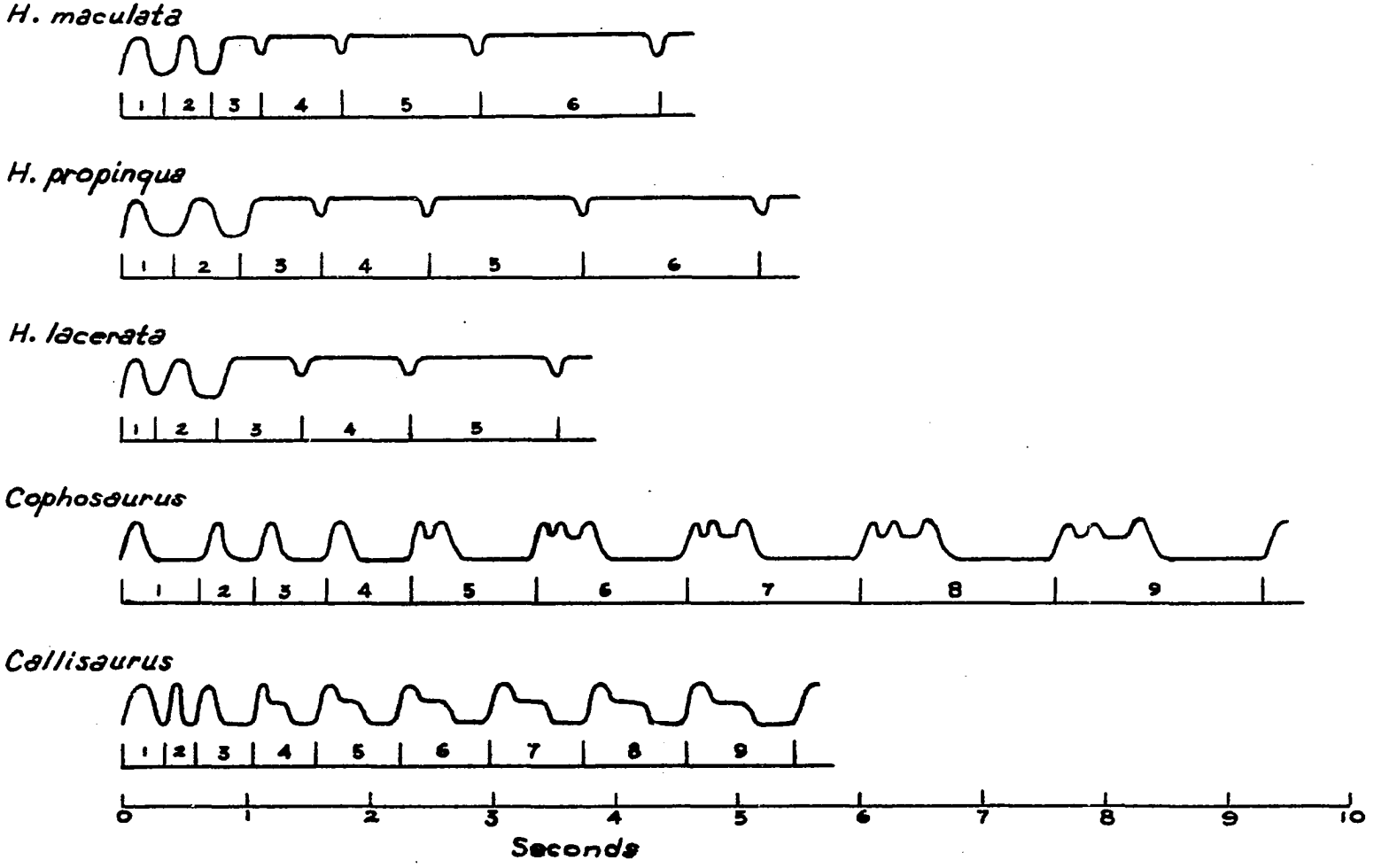



Fig. 10. Display action pattern graph of the sequence of push-up movements of the species studied.

the unit there is a pause before the next unit begins. This pause is considered as a terminal portion of a unit. Therefore, a unit consists of one or more movements and includes the following pause that occurs before movements initiate the next unit. Neither the lowering of the body at the beginning of a sequence of units nor the raising of the body at the termination of a sequence is considered as part of a unit.

Units of Holbrookia were simple and of two types. One was a full rise and immediate return; the other was a short rise from half-lowered position with a longer pause before return to the half-lowered position.

Cophosaurus exhibited three types of units: the simple single full rise and return; a double high bob, in which the lowering between raises was only one-half; and a triple high bob. In the latter, the lowering between raises was only one-half, and the third rise, which was slightly higher in amplitude than the other two, was preceded by a slight pause.

Two types of units were present in Callisaurus. One was the simple full rise and return. The other was a full rise, followed by a one-half lowering, short pause, and return to original position, with a following pause.

Sequence of movements. A sequence of movements consists of the order in which the units appear and the number of units performed in succession. In each of the genera studied, the sequence could be divided into two parts: an introductory portion and a regular part. The introductory portion differed considerably from the regular part, and in both Callisaurus and Cophosaurus was found to be more variable,

particularly at the beginning. Figure 10 illustrates the sequence for each species.

In each species of Holbrookia, the introductory units were consistently two, but the regular units ranged in number from one to six. However, less than ten per cent of the sequences observed contained more than three regular units.

Cophosaurus exhibited a variable beginning to the sequence, some individuals exhibiting one or two extra single units preceding the sequence as given in Fig. 10. All individuals observed, however, showed a series of four single units, followed by a double unit and a variable number of regular units. The regular units ranged from one to eight, with 59.1 per cent of the sequences ending with either three or four regular units.

Sequences of Callisaurus, as with Cophosaurus, began with an occasional extra single unit, but all exhibited the pattern shown in Fig. 10. Three single units were followed by a varying number of regular units, which ranged from three to nine. Three-fourths of the sequences contained either four, five, or six regular units, five units being the number in over 40 per cent of the total sequences.

A unit was added to the beginning of the sequence of Cophosaurus and Callisaurus occasionally when either of these genera exhibited maximum display. This unit is termed "push-out" and appears only during exceptional assertion or challenge effort. The movement begins with the body being slowly raised and extended forward. The forward movement continues until it appears that the lizard loses its balance. A slight forward step is taken with one foot, and the forepart

of the body is lowered and retracted. This may be repeated again three or four times, moving the lizard slowly forward for several steps. The push-out is immediately followed by a strong push-up series. Curling and waving of the tail may accompany the push-out and push-up. Although most commonly noted in males of Callisaurus and Cophosaurus, the push-out has been observed in female Cophosaurus and in male H. propinqua, though rarely in the latter species.

Cadence. An attempt was made to obtain the cadence, or timing, of units by the method used successfully by Carpenter and Grubitz (1961) for Urosaurus. It was found that stop-watch timings for individual units were difficult to make accurately because of the rapidity and complexity of the push-up pattern. Therefore, the times given in Table 1 have been taken from photographed sequences. Table 1 gives the means in seconds for each unit of the sequence for each species studied.

With the exception of the first two introductory units, there is an increase in length for each subsequent unit. The appearance of the sequence for each form is one of initial rapidity, followed by obvious slowing. Only in Callisaurus do none of the units exceed one second in duration, the entire sequence appearing as a continuous motion. Obvious pauses between movements are discerned in the patterns of the other species.

In Cophosaurus and Callisaurus, the second unit of the sequence is considerably shorter than the first. In Holbrookia, this is the case in H. maculata, but H. propinqua has the second unit approximately equal to the first and H. lacerata has the second unit noticeably longer than the first. Thus, although the pattern is similar in the three species

TABLE 1

CADENCE OF PUSH-UP UNITS IN SECONDS AS DETERMINED BY MOTION PICTURE ANALYSIS

| | Order of Units in Sequence | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| H. maculata | 0.44 | 0.32 | 0.47 | 0.67 | 1.01 | 1.43 | | | |
| H. propinqua | 0.50 | 0.49 | 0.62 | 0.88 | 1.27 | 1.45 | | | |
| H. lacerata | 0.32 | 0.48 | 0.66 | 0.88 | 1.20 | | | | |
| Cophosaurus | 0.68 | 0.41 | 0.58 | 0.68 | 1.00 | 1.19 | 1.44 | 1.59 | 1.70 |
| Callisaurus | 0.33 | 0.22 | 0.47 | 0.49 | 0.62 | 0.72 | 0.77 | 0.81 | 0.86 |

of Holbrookia, the cadence differs sufficiently to cause each to be distinct.

## Assertion Display

Display of low intensity, not necessarily directed at another lizard and often performed in the absence of other lizards, was termed assertion display. This is contrasted with aggressive high intensity display, challenge, which is directed at another male lizard (Carpenter, 1962a). Generally, the body was not laterally compressed, the dewlap was not expanded, and the lizard did not rise up with arched back and lowered head. Assertion display was the most common form of display and was performed by both sexes, most often exhibited when a lizard stopped after moving from one location to another. This display seemed to serve as a territorial function, advertising the presence of the lizard. Dominant males and gravid females asserted more frequently than subordinate males and non-gravid females. The sequence did not seem to be shortened appreciably, nor did the cadence appear changed from that of the challenge. At times, however, the assertion was exhibited simply as a nodding of the head, often when the lizard was prostrate. Frequently, other lizards responded to the assertion of one lizard by themselves asserting. This did not appear to be response to a challenge, but a reply to the asserting lizard. Members of one species doing an assertion display might cause response in those of other species. Sometimes the assertion caused a chain reaction, with one lizard after another performing push-ups or head nods.

The most intense assertions were performed by dominant male lizards. Holbrookia and Callisaurus generally asserted from the ground

level or some slight elevation, whereas Cophosaurus performed most often from raised objects. A dominant Cophosaurus patrolled a territory, moving from one high point to another, and asserting strongly from each position as soon as he arrived there. In Cophosaurus and Callisaurus, the dewlap was partly expanded in dominant males and gravid females during strong assertion display.

Hatchlings were observed asserting within five minutes of emergence from the egg. The pattern of the assertion was that of the adult. This was not a pattern learned from other lizards, for young which were hatched and kept from view of other lizards still exhibited the pattern of push-up characteristic for the species.

## Tail Display

A feature of display common to both Cophosaurus and Callisaurus is the curling of the tail over the back (Fig. 11). Although Holbrookia species may raise the tail at times, it is never held in the symmetrical curl exhibited by the other genera. In H. lacerata, the tail may be raised with the tip curving toward the head of the lizard (Fig. 11). In H. propinqua and H. maculata, the tail may be raised vertically, but the tip does not curve toward the head.

It is evident that curling of the tail is employed more frequently by those forms which possess a distinct black and white subcaudal pattern. These forms not only curl the tail when eluding pursuit, but also utilize this display when moving about undisturbed. Frequently, tail display is associated with assertion display. The use of the tail, therefore, may function as part of the advertisement of the lizard, making it easier for males and females to find each other during mating season,

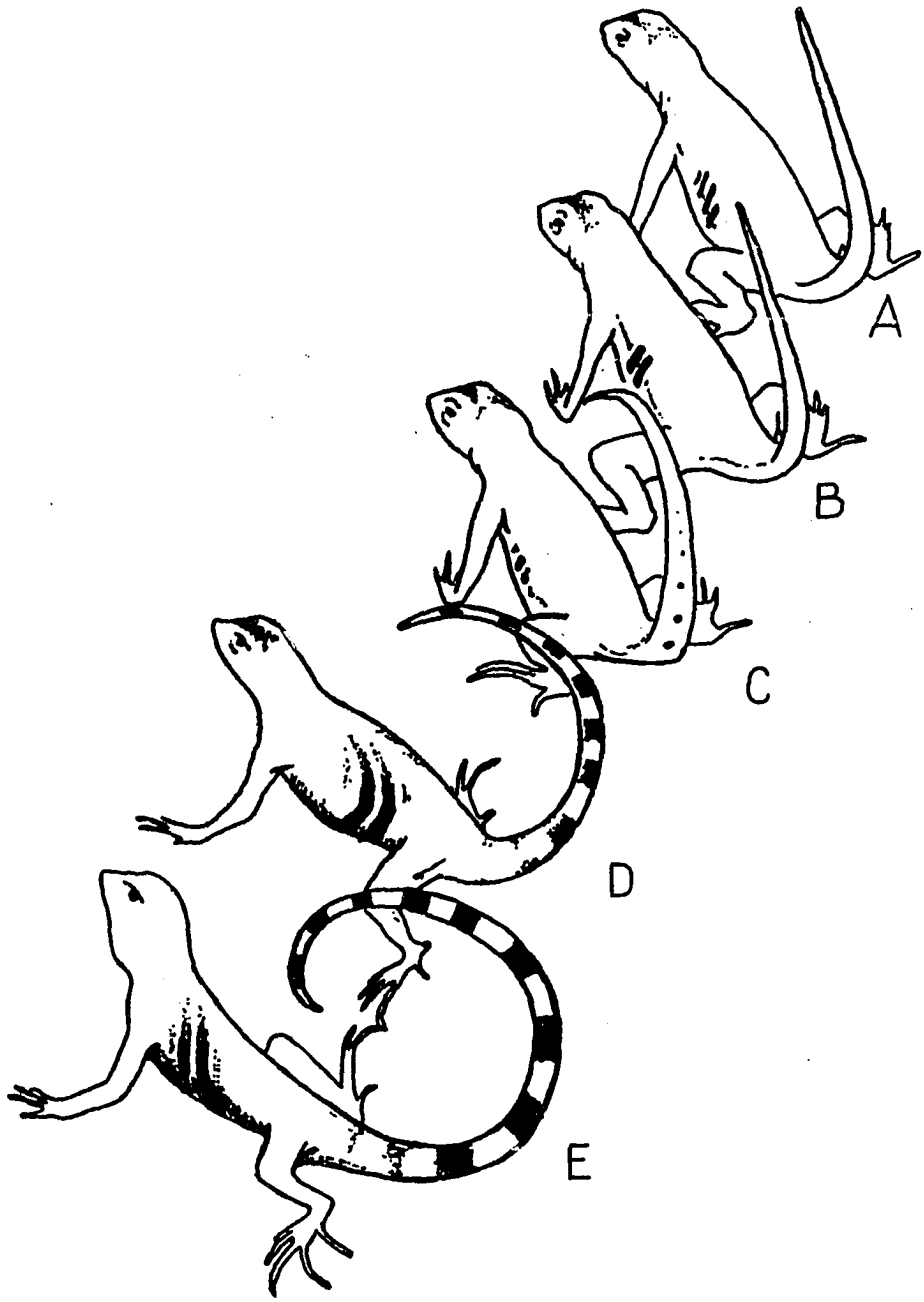



Fig. 11. Tail display in the species studied, illustrating differences in the attitude of the tail: A. H. propinqua, B. H. maculata, C. H. lacerata, D. Cophosaurus, E. Callisaurus.

and also as a territorial declaration of one male to another. Evans (1953) found that tail curling is another iguanid, Liocephalus, was used as an integral part of the social structure only. It was not practiced when other individuals of that species were out of sight.

Tevis (1944) suggested two functions for tail curling in Callisaurus. One, the tail wagging probably directs the predator's initial attention to this organ, which is detachable. Second, the attention of the observer is on the waving tail with its conspicuous black bars and, when the lizard runs, the gaze remains on the spot where the tail had been. When the tail is depressed, the lizard seems to vanish, so much does its dorsal coloration blend into the surroundings.

The black and white subcaudal pattern is similar in Callisaurus and Cophosaurus, but the subcaudal markings of H. lacerata are quite different (Fig. 11). H. maculata and H. propinqua lack any black spotting on the undersurface of the tail. Axtell (1956) stated that he noted more use of the tail in H. lacerata than in the other species of Holbrookia, and that the tail was used presumably ". . . in defensive posture."

Elevation of the tail in Callisaurus and Cophosaurus is first indicated by a slight curl of the tip of the tail. This portion of the tail may be curled and uncurled or may be raised slightly and flipped from one side to the other. This indicates a buildup of nervous tension. The tail is then raised and curled over the back, and the lizard usually moves to another location.

Tail raise in Holbrookia does not exhibit the flexibility shown by the other genera studied. Nervous excitement may be shown

by the tail tip twitching, but it is never half-curled and flipped from side to side.

Tail curling attitudes are slightly different in Callisaurus and Cophosaurus (Fig. 11). In Callisaurus the tail is raised in a tighter curl and is carried farther forward. The tail raise of H. lacerata is less of a curl than either of these.

It is typical for the tail to be waved from side to side in Callisaurus while curled. In Cophosaurus, tail waving is much less employed, and occurs only upon provocation in Holbrookia.

# CHAPTER III

## SEXUAL BEHAVIOR

### Courtship And Mating

Noble and Bradley (1933) described courtship and mating in various families of lizards. Their findings indicate that patterns of behavior exist which differ among families, but vary little among genera and species of any one family. The courting behavior is stereotyped and, as pointed out by these authors, should not be confused with the less stereotyped and more spectacular fighting reaction. The challenge or fight response consists of lateral compression of the trunk extension of dewlap, arching of back, lowering of head, and usually assertion push-ups. Courtship, on the other hand, in Iguanidae, generally consists of less display on the part of the male. He lowers the head and arches the back as in the fighting response, but does not compress the sides greatly or expand the dewlap to the utmost. The head may nod rapidly and the male may walk to the female with, as Fitch (1956a) described, ". . . a peculiarly relaxed and loose-jointed, slithering gait. . ." He may then touch the side of the female with his snout or grasp the skin of the neck or side with his jaws. His body may lie upon the female with his tail twisted beneath hers until the cloacal openings meet. The hemipenis is inserted and coition occurs. The courtship of

Holbrookia, Cophosaurus, and Callisaurus follows this general iguanid pattern with minor variations.

Courtship patterns vary little among the five lizard species studied. In any one species, however, there may be a variety of courting procedures. In no case is the courtship elaborate; usually it consists simply of a male investigating another lizard and, finding it his species and the opposite sex, grasping the skin of the back of the female in his jaws and attempting to mount her. In each case the biting grasp of the male is on the region of the back just above the insertion of the foreleg.

Investigation of another lizard by a male consists generally of the male noting the presence of the other lizard and becoming more alert. The forepart of the body is raised and the head held erect. The male approaches the other lizard with back slightly arched and the head lowered. The head may be nodded rapidly, the number of nods for each sequence being 6 to 25; the time for each sequence varying from approximately one-tenth of a second to more than one second. At times the cloacal region and the undersurface of the thighs are dragged on the substrate as the male moves forward. When the female does not move away, give active rejection behavior, or complete submissive posture, the male may nudge the cloacal area of the female, nudge her in the side, or test her with his tongue on the side of the body or the head. The male then either desists in his attentions or attempts to secure a grip on the back above the shoulder. If the female stands passively, the male may mount and attempt copulation.

The above description of courtship on the part of the male should be looked upon as an "ideal" one. Usually, there were variations from this pattern. The male might simply rush at the female from a distance of more then eight feet and grasp her in the shoulder region. In most of these cases, the female resists violently, often escaping the attentions of the male. Frequently, the male, upon first seeing another lizard, performs an assertion push-up and waits for a signal reply from the other. If the other lizard replies in like manner, this indicates another male or a non-receptive female and might cause the male to lose interest or approach aggressively. If the other lizard flattens completely it indicates either rejection by a non-gravid female or a submissive male. In either case the male usually pays little more attention. The other lizard might stand still and allow the approach of the male with neither of the above behavioral responses. At the approach of the male, the female might orient her body so that the posterior is presented to the male with the tail raised or moved in a manner characteristic of the species involved. This constitutes active rejection by a female. The male usually nuzzles the female in the cloacal region during this posture and desists in his courtship. At times, however, no rejection postures were successful, for the male persisted in his attempts to mate.

Courtship and mating will be described for the species studied, in order to present variations and similarities in the behavior of each species.

Holbrookia maculata. In 16 courtships which were carried as far as the neck grasping stage, 10 were directed to non-gravid females,

but in only one did coition occur. In every case observed, except one, the male rapidly nodded before grasping the female. In half of the observations males showed no preliminary courting actions near the female, but upon seeing her, nodded their heads, dashed to the female and grasped her forthwith. On two occasions the male approached the female with rapid nods and pushed his nose into her cloacal region and in one instance nudged her in the side. Female response to male's grasp was to reject the male by actively rolling over and twisting in such a manner that the male's hold was broken. Three of the instances noted were of males grasping gravid females. These females most violently opposed the grasp of the male, one even retaliated by breaking loose and grasping the male in the shoulder region and retaining the grip for three minutes.

In coitus, the male inserted the hemipenis for 20 seconds, with slight spasmodic movements of the pelvic region and hind leg, which was over the back of the female. Retraction of the hemipenis was accompanied by the posterior of the male being highly elevated, the tail held in an arching curve.

One instance was noted of a male H. maculata grasping a female H. lacerata.

Two cases of attempted homosexual matings were seen. In both of these the male had grasped another male in the side, but the second male reacted so violently each time as to dislodge the attacking male before further phases of mating could be attempted. In one of these encounters the attacking male released one male, ran and grasped another male that passed by.

Holbrookia propinqua. Thirty-seven courtships were observed in which the male grasped the female. Of these, 20 were with non-gravid females, 16 with gravid females, and one with a female whose status was undetermined. Courtship proceeded through coition with seven of the non-gravid females and with two of the gravid females. Most of the rejection began with a tussle which caused the male to relinquish his grip of the female. In 12 cases the male rushed at the female with no preliminaries, grabbing her in the shoulder region. It was noted that the male approached the female with rapid nodding of the head on 16 occasions. These approaches were without the aggressive sidling and display employed against other males. The male occasionally nudged the female in the posterior when he came to her. Once a male came toward a female from the front with his belly pressed to the sand, moving sinuously as he approached.

The time for actual coition is quite short, being close to, or less than, one-half minute, after which the male lifts his posterior and retracts the hemipenis while still retaining his grip in the female.

There were three instances noted when a male H. propinqua courted and grasped a female of another species. In each case it was a female H. maculata, and in each case the female successfully repelled the male's advances by rolling over and twisting until freed. No homosexual matings were noted.

Holbrookia lacerata. Only three courtships were observed in H. lacerata and copulation occurred in none of these. The male approached with rapid nods, as in the other species. Once, the male did not grasp the female, once he grasped her in the side, and once above the foreleg. The following courtship occurred on May 15, 1962.

The male lacerata approached the female with rapid nods. The female had her chest down, posterior raised slightly and tail curled upward. The male nosed the cloacal region of the female once, stopped, and then nosed it twice more. He rushed forward and grasped the female in the shoulder region. The female struggled and broke loose. The male desisted.

Cophosaurus texanus. Rapid head nods and shoulder grip appeared to be the same as in the preceding species. A bit more display on the part of the male, however, was noticed, particularly some lateral display involving the partially expanded dewlap. Most of the males ran to the females from some distance and grasped them quickly or chased them. The duration of coition is short in this species, too. On two occasions a male, the same one in both cases, lay flat upon the back of a female and tried to twist his tail under hers without securing a neck grip with his jaws. In neither case was he successful. Stroking of the female's dorsal pelvic region was observed in one instance. This appeared to calm the female, which had been trying to free herself. Only one leg was involved, the motions were made as if the male were stroking the back of the female with the undersurface of the leg and the foot.

One homosexual mating was observed. In this the dominant male grasped a subordinate just above the insertion of the foreleg, straddled the body, and vibrated the underside of one leg and then the other on the pelvic region of the attacked male. The dominant twisted his tail beneath that of the subordinate and curled his pelvis to one side, attempting copulation. The subordinate broke loose. The dominant stood with pelvis held high, tail arched up, while the hemipenis was retracted.

An intergeneric homosexual mating attempt was witnessed by Dr. Charles Carpenter (personal communication) on July 31, 1960. It involved a male Cophosaurus and a male Callisaurus. The Cophosaurus displayed vividly and presented himself laterally to the Callisaurus; then rushed in and bit him. The Callisaurus tried to roll over and escape, but the Cophosaurus retained his grip on the skin of the posterior central part of the shoulder area. The Cophosaurus straddled the back of the Callisaurus, made hopping motions with the hind feet, and tried to move into mating position. Callisaurus was not submissive and stood with legs fully extended. Copulation was not successfully accomplished.

Callisaurus draconoides. Only two courtship attempts were observed, both of which were repulsed by the female. In each, the male approached with rapid nods and with some display.

## Female Response to Courtship

In none of the observed attempts at copulation could any of the female's behavioral posturings or actions be noted that appeared to be deliverately aimed at attracting the male. Only passive acceptance or token resistance on the part of the female were noted when coitus did occur. Most often, males appeared more eager to engage in mating with those females which moved away or resisted the initial advances. Evans (1935) suggested, from his study of Anolis carolinensis that ". . . the mere flight of the female from the performing male quite probably signifies acceptance of the male and is therefore a definite part of the complete courtship pattern and should be considered as an important phase of the mating instinct. Although her response is a negative one we need not assume that it is of negative value in leading the male to

her." In Sceloporus, Fitch (1940) stated, ". . . it is noteworthy that mating normally involves pursuit and struggle. A female physiologically ready to mate struggles only perfunctorily, whereas one at any other stage in the annual breeding cycle resists with such vigor as to repulse the male." It was thus with the species of Holbrookia, Cophosaurus, and Callisaurus, in which eager males most often grasped females apparently unwilling to mate and were dislodged only after a struggle which involved much thrashing about and rolling over. No one type of female rejection seemed to work all of the time. Certain rejection attitudes were used by all of the species, but some were utilized by only one or two species.

Female rejection, other than the tussle which ensued after the female was grasped, consists of the following: running or moving away, flattening with or without tail wave, belly slide, raising the body high and orienting caudally at the male, and aggressive behavior by gravid females.

Running away or moving away from contact with the male was noted in less than one-half of the encounters in all species, except Cophosaurus, where 80 per cent of the non-gravid females moved off.

Flattening of the body in submissive pose was general in all but Callisaurus. The usual response for submissive Cophosaurus and H. maculata was to keep the tail down. H. lacerata always curled the tail upward and H. propinqua raised the tail most of the time. H. lacerata held the tail erect and waving. H. maculata held the tail just above the surface of the substrate and waved it rapidly from side to side.

One response to cloacal nuzzling by the male was for the recipient female to flatten and slide along on the belly, with the tail raised and usually rapidly waving. This was noted once in Cophosaurus and once in H. lacerata; more frequently in H. propinqua and H. maculata. Both males and females exhibited belly sliding. The sliding forward was in short spurts of only a few inches. This behavior acted as a deterrent to the courtship of some males but appeared to be a stimulus in a few cases, the male rushing forward and attempting to mate. That this is not part of the regular behavior pattern of a receptive female is shown by the frequent use of this pattern by males, and in none of the attempted matings which resulted from this was copulation successfully completed. In each case the female twisted, rolled over, and shook off the male that had grasped her.

Only in Callisaurus did it appear characteristic for the non-gravid female to rise up on tiptoe when courted by a male.

It was noted in each of the species that often a male would approach another lizard and place his snout in the cloacal region of the other lizard. The male would then either pay no further attention to the lizard or would appear to butt the other lizard in this region. The butting occurred only if the other lizard was a female. The female responded to cloacal butting by rising on fully extended legs, often placing the caudal area higher than the rest of the trunk, orienting caudally at the aggressor, and waving the tail from side to side. As the male moved about, the female also shifted so as to maintain this orientation. Caudal orientation toward the male, along with rapid waving of the tail, could be a deterrent to a mating attempt by the male, since

he must grasp the skin of the shoulder of the female before copulation can be consummated. The tail waving could well act as an added dissuader. The black and white pattern of the undersurface of the tail of Callisaurus and Cophosaurus, and to a lesser extent in H. lacerata, would add to the effectiveness of this display. In each of these forms the tail is curled upward and waved from side to side, thereby giving more emphasis to the patterned undersurface.

The behavior of gravid females of each of the species studied has been shown to change from a passive role into an aggressive type quite similar in many respects to the behavior of agonistic males. Fitch (1940) commented upon the growing intolerance of gravid female Sceloporus occidentalis for males. ". . .The aggressiveness of such females toward males contrasted with the timidity of those which had not yet mated."

By becoming aggressive, the female actively discourages mating by the males; she also advertises her sex by color display and posture, which does not release the territorial aggressiveness of the male, and allows the female to go unchallenged and unmolested during her period of egg development.

In each of the species studied, with the exception of H. lacerata, the gravid females performed full assertive displays with compressed sides, body raised from substrate, lowered head, arched back, and extended dewlap. The accompanying push-ups and rapid nods accentuated this display. Challenge and active aggression were regularly part of the behavior of gravid females. H. lacerata females showed only the lowered head and arched back portion of the display.

Callisaurus and Cophosaurus were alike in their display. Each has a dewlap that is quite prominent when extended in comparison to the much smaller dewlap of H. lacerata, H. propinqua, and H. maculata. When females of Callisaurus or Cophosaurus displayed, it was usually a lateral presentation to the opponent, this orientation being held during the display. The trunk of the lizard was compressed and the dewlap expanded. In both of these species the dewlap of the gravid female is pink or orange. The dewlap and the prominent spot of color on the side behind the front leg are conspicuous in this lateral presentation. The tail may be curled and waved, presenting the black and white pattern of the underside.

Gravid female H. maculata usually raised the body from the substrate with the legs about two-thirds extended, back arched, head lowered, the small dewlap area expanded, and presented caudally toward the male, with the tail raised and held motionless. The posterior was moved so that it was continually oriented toward the male. At times the lizard would turn and present laterally to the male. The dewlap in these lizards was inconspicuous and was not colored. The red stripe on the posterior of the thigh and at the lateral base of the tail was quite conspicuous in the caudal display, especially when it was associated with the surrounding yellow. The lateral red stripe was outlined with yellow, making it more distinct in lateral presentation. The yellow cheeks also showed well in lateral display.

Gravid female H. propinqua exhibited a definite use of their color patterns during rejection displays. The yellow cheeks, lateral area, back of thighs, and base of tail tended to exaggerate the prominent

red stripe which was present along the fold of skin on the ventral edge of the side of the body, along the posterior of the thigh and on the lateral base of the tail, similar to H. maculata. The characteristic posture of a disturbed gravid female was to raise the body with back arched and head lowered, the sides compressed, and the lizard laterally presented. This lateral presentation was different from the others in that the body of the lizard was curved, with the head and pelvic region pointed somewhat toward the male (Fig. 12). The trunk was tilted away from the adversary, exposing the lateral color stripe. At the same time the tail was characteristically curved upward and away from the male, generally forming an arch with the tip touching the substrate. This exposed to the male the colored undersurface of the proximal part of the tail and the colored stripe on the posterior of the thigh. The head was nodded rapidly at the male, and the two often moved around in a tight circle, maintaining the postures and nodding.

The effect of characteristic posturing in each species appears to be to display the colored areas most effectively to the male. These colored areas are enhanced by enlargement of the tinted surface and by the emphasis of contrasting color, yellow. It is noteworthy that gravid female H. lacerata had none of the red markings and showed no pasturing which differed from that employed by males and non-gravid females.

In some instances certain gravid females performed a peculiar "dance." This was noted in each of the species, except H. lacerata. It is characterized by the female rising high with arched back and moving about the male with a peculiar stiff-legged, jerky gait, often with lateral presentation and display. The female may move away from the



Fig. 12. Gravid female rejection posture of H. propinqua: upper figure, female; lower, male.

male in this manner, still retaining the lateral presentation, and may reverse the presentation from one side to the other repeatedly. The female also may turn the posterior to the male and raise and wave the tail while performing. The term "sidlehopping" has been given to such action and was described by Carpenter for Sceloporus merriami (1961a) and for S. undulatus (1962a).

Noble and Teale (1930) attributed this behavior in Sceloporus undulatus to a willingness to mate, but later Noble and Bradley (1933), for the same species, stated that this never seemed to stimulate males and that they could find no evidence that this behavior indicated willingness to mate on the part of the female. They further remarked, "It has nothing to do with ovulation, for eggs were not found in the oviducts of one 'hopping' female which was dissected." Fitch (1940), in discussing S. occidentalis, pointed out that there is a definite association between such behavior and the reproductive condition of the female by stating, "While non-gravid females may occasionally show such behavior, it seems to be characteristic of those which have been impregnated, and replaces the instinct to crouch against the ground or to avoid the attentions of a male before impregnation has occurred. I have frequently seen the hopping reaction in courted females in the wild, and in every instance the female was distended by eggs, and obviously gravid."

Sidlehopping and jerky gait are not the responses generally given by females of Holbrookia, Cophosaurus, or Callisaurus to the close approach of a male, rather, it is exceptional to observe these fully expressed. More often, only a part of this display will be noted, such

as a stiff-legged step or a single hop. Seven observations were made during the course of the study in which there was obvious sidlehopping or stiff-legged walk. Gravid female H. propinqua often used a markedly stiffened gait when circling and displaying at an aggressive male. In every observation noted in which there was exaggerated sidlehopping or other similar behavior, the female was either gravid or had recently laid. Three individuals of H. maculata were noted sidlehopping: two within a week after oviposition and one three weeks prior to nesting. One female Cophosaurus exhibited sidlehopping on several occasions. She laid three clutches of eggs during the summer of 1962 and sidlehopping was observed a few days before and after egg-laying. A single female of H. propinqua and Callisaurus exhibited sidlehopping. In both cases the females were gravid.

The "hopping" female Sceloporus, dissected by Noble and Bradley (1933), upon which they based their statement that "hopping" has nothing to do with ovulation, could have recently nested and still retained the gravid behavior. That sidlehopping occurs in female Sceloporus nearly ready to lay may be inferred from the statement by Fitch (1940) in which he pointed out that each female that sidlehopped was ". . . distended by eggs."

It appears that the type of rejection, sidlehopping, or modifications thereof, is employed by females which either have recently laid their eggs or are about to nest. Sidlehopping is a more active rejection than usually employed by unreceptive females and seems to be associated with a general nervousness observed in females near the time for oviposition. Non-gravid females may reject the advances of males, but may employ other means of rejection.

From the time of insemination, increased restlessness and nervousness is evident in gravid females. This is shown in increased movement, assertive head nodding and push-ups. In the days immediately preceding oviposition the lizard becomes extremely agitated at the approach of another lizard and will often aggressively attack and drive away any lizard that ventures near.

The length of time between the onset of aggressive behavior and oviposition and the duration of the aggressive behavior following egg laying could not be determined precisely because of the dearth of females that nested.

Aggressive behavior of females appeared about 30 days before oviposition, but was observed for only two or three days following egg deposition. It appears that aggressiveness in gravid females discourages courting in males. This behavior is soon lost after oviposition and the female may become receptive.

## Sex Recognition

In the family Iguanidae, sex recognition has been attributed primarily to heightened color in the male and prominent pattern differences between the sexes. Greenberg (1945), suggested that the yellow-orange color of the gular region of the male Crotaphytus was the significant recognition feature, and that when the gular region was hidden by a prostrate subordinate male, this male would be courted, rather than attacked, by the dominant male. Fitch (1954) attributed sex recognition in the family Scincidae to the reddish color of the head of the male during breeding season. He states, "Their reddish facial suffision serves as a social releaser which elicits hostile

behavior and facilitates sex recognition," and later (Fitch, 1958) emphasized the importance of color in sex determination in the teid lizard, Cnemidophorus sexlineatus, where blue and green suffuse the sides and flanks of the male.

Evans (1938b) characterizes sex recognition in Anolis as a combination of color and postural behavior, the expansion of the colored dewlap of the male eliciting a response characteristic of either male or female noting this. He even suggested that sexual selection on the part of the female may have played an important part in the evolution of the dewlap. The value of both postural behavior and color pattern in sex recognition was pointed out also by Carpenter (1961a) for Sceloporus merriami.

Species of the genera studied showed their ability to determine the sex of another individual quite readily. The aggressive male usually asserted laterally at an intruding individual, showing off at best advantage the color patches and ventrolateral bars as the trunk was compressed, and dewlap as it was expanded. If the intruder did not respond in like manner, the male approached the other lizard head on, with the back arched and the head lowered, the head being bobbed rapidly in short series as the lizard moved forward. If the intruding lizard did not display laterally, the colors and pattern of lateral bars would be inconspicuous, and the male would continue rapid nodding at the intruding lizard until it assumed one of several subordinate postures or moved away. There were times, however, when a male would give only a perfunctory rapid head nod and bolt directly at a newly arrived female and grasp her by the skin above her front leg. These dashes have been made from a

distance of over three feet. It appeared, therefore, that the stimulus was visual: color and pattern, or behavior, or a combination of the two.

In order to test the adequacy of the accentuated ventrolateral marks and colors alone as means of sex recognition, four Cophosaurus and four H. propinqua were selected and painted to represent the opposite sex. It was noted in both Cophosaurus and H. propinqua that there was a distinct observable difference in the attitude of a territorial male toward another male or a female of his species. In both species there was little tolerance for a male within the territory of another male. A female, however, was not only generally tolerated, but also courted.

Two male (Nos. 1, 4) and two female (Nos. 20, 70) Cophosaurus were selected, all for their known vigor, and one (No. 20) because she was gravid. The two male H. propinqua (Nos. 7, 88) selected were aggressive individuals. One of the two females (No. 80) was gravid and the other (No. 87) was not.

The males of Cophosaurus were painted gray to obliterate markings and color. The females were painted with exaggerated black ventrolateral bars and large blue color blotches as is normal in the male, and the buff and orange outline of the ventrolateral stripes was placed on the dorsum.

The colors of the male H. propinqua were painted to simulate the female; the dark lateral spots were subdued. The female H. propinqua were painted so as to heighten the effect of the lateral spots as well as the dorsal pattern.

These lizards were placed into the enclosure, which housed an established population of both H. propinqua and Cophosaurus at 5:10 P.M.

on August 7, 1962. The day was clear and warm, and the occupants of the enclosure were alert and active. The test lizards were released singly and the reactions of the other lizards present were recorded.

The gravid female H. propinqua was approached by a male H. propinqua that came up from the side and placed his snout into the cloacal region of the female. The female raised up, arched back, compressed sides, lowered head and raised the tail and curled it away from the male. She turned her head in toward the male, rapidly nodded, and made a threatening movement toward the male. He dashed in, grabbed the female by the shoulder, and dragged her for a short distance. The female struggled violently and broke loose.

Less than five minutes later this same female was grasped in the shoulder region without previous display by a different male. The female halted and assumed the typical gravid rejection posture described above, with rapid nods of the head. The male did not desist in his mating attempt and grabbed the female again. The pair struggled for 30 seconds, at times rolling over completely. The female broke loose, arched back, lowered head, and assumed the rejection posture again. The male moved away.

Male 88 H. propinqua that was painted to resemble a female was challenged by an aggressive male H. propinqua. The aggressor approached the male 88 with full assertion, compressed sides, head lowered and with series of rapid nods. The approach was sidling, in which there was continued lateral presentation, with the aggressor leaning toward his opponent, the near hind leg being dragged. In all, it was the typical challenge display of one male toward another male.

Male 88 ran away and was actively chased from the vicinity by the aggressor.

There was no interaction at all between the Cophosaurus.

The following day these interactions were noted.

The gravid female H. propinqua aggressively chased away both males and females from her vicinity with full display and rapid head nods.

Male 7 H. propinqua aggressively chased away the male 88 H. propinqua.

The dominant male 61 H. propinqua challenged and chased away both of the above male H. propinqua.

Male 88 H. propinqua was challenged and chased by the male 11 H. propinqua.

The non-gravid female H. propinqua was neither challenged nor courted.

Dominant male 5 Cophosaurus challenged the male 4 Cophosaurus (pseudo-female) with full lateral display and push-ups. He leaned far toward male 4 and sidled at him aggressively. Male 4 ran rapidly away.

The dominant male 5 Cophosaurus later presented laterally at the female 70 Cophosaurus (pseudo-male). He moved in with rapid head nods. The female raised the body, lowered head, expanded dewlap, arched back, and did a shallow assertion push-up. This is gravid female behavior. The male desisted.

Dominant male 5 Cophosaurus challenged the male 1 Cophosaurus (pseudo-female) with full lateral display, push-outs, and push-ups. He then charged headlong at male 1 from three feet away, which caused male 1 to flee.

Apparently, recognition of the sexes in both Cophosaurus and H. propinqua does not depend primarily on the color and pattern, since in every case noted the change in pattern and color made no difference in the behavior of other lizards toward the individual so altered.

In other genera, the dimorphic color may assume more of a role in sex recognition. Noble and Bradley (1933) found that female Sceloporus undulatus, painted to simulate males caused attack behavior in other males, whereas males with the ventral color marks obliterated were courted.

The recognition of sex appears to depend to a large extent on the behavioral postures of the lizards. Sidling, with exaggerated display, push-up, and rapid head nod is characteristic of an aggressive male, whereas the lack of this display characterizes the female or the subordinate male.

The various species have variations of this general theme, some of which appear to be characteristic for a particular species. Observations of enclosed populations were made concerning the four status groups of each species: agonistic males, submissive males, non-gravid females, and gravid females. Percentages of each of several behavioral features were calculated and are given in Table 2. No agonistic H. lacerata were noted; therefore could not be entered in table.

Table 3 summarizes the pertinent points of similarity and difference in the four status groups within each species. It can be seen that the submissive males and the non-gravid females share many of the behavioral traits which are at variance with those shared by the agonistic males and the gravid females. These same groupings are

TABLE 2

PERCENTAGE OF LIZARDS INVOLVED IN VARIOUS BEHAVIORAL ATTITUDES AND MOVEMENTS OF BODY PARTS

| | | Placement | | Body | | Tail | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Moved Away | Remain | Flat | Raised | Not Raised | Raised | Still | Moved |
| H. lacerata | S | 66 | 34 | 67 | 33 | 0 | 100 | 16 | 84 |
| | A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | N | 14 | 86 | 60 | 40 | 0 | 100 | 40 | 60 |
| | G | 0 | 100 | 0 | 100 | 0 | 100 | 0 | 100 |
| H. maculata | S | 30 | 70 | 73 | 27 | 46 | 54 | 46 | 54 |
| | A | 0 | 100 | 0 | 100 | 92 | 8 | 92 | 8 |
| | N | 26 | 74 | 68 | 32 | 37 | 63 | 24 | 76 |
| | G | 4 | 96 | 0 | 100 | 52 | 48 | 83 | 17 |
| H. propinqua | S | 70 | 30 | 100 | 0 | 80 | 20 | 58 | 42 |
| | A | 0 | 100 | 0 | 100 | 67 | 33 | 89 | 11 |
| | N | 53 | 47 | 79 | 21 | 14 | 86 | 0 | 100 |
| | G | 10 | 90 | 4 | 96 | 30 | 70 | 94 | 6 |
| Cophosaurus | S | 88 | 12 | 100 | 0 | 88 | 12 | 88 | 12 |
| | A | 0 | 100 | 0 | 100 | 91 | 9 | 91 | 9 |
| | N | 80 | 20 | 80 | 20 | 90 | 10 | 80 | 20 |
| | G | 19 | 81 | 12 | 88 | 75 | 25 | 75 | 25 |
| Callisaurus | S | 64 | 36 | 100 | 0 | 86 | 14 | 67 | 33 |
| | A | 0 | 100 | 0 | 100 | 60 | 40 | 60 | 40 |
| | N | 55 | 45 | 18 | 82 | 27 | 73 | 55 | 45 |
| | G | 0 | 100 | 0 | 100 | 60 | 40 | 80 | 20 |

S = submissive male; A = agonistic male; N = non-gravid female; G = gravid female

TABLE 2 (Continued)

| | | Display | | Head | | | | |
|---|---|---|---|---|---|---|---|---|
| | | No | Yes | Push-up | Rapid Nod | Neither | Attacked | Number of Observations |
| | S | 100 | 0 | 16 | 0 | 84 | 0 | 6 |
| H. lacerata | A | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | N | 100 | 0 | 14 | 0 | 86 | 0 | 7 |
| | G | 86 | 14 | 14 | 0 | 86 | 0 | 7 |
| | S | 100 | 0 | 0 | 0 | 100 | 0 | 26 |
| H. maculata | A | 0 | 100 | 77 | 15 | 8 | 32 | 13 |
| | N | 100 | 0 | 0 | 0 | 100 | 0 | 19 |
| | G | 13 | 87 | 26 | 4 | 70 | 0 | 23 |
| | S | 65 | 0 | 0 | 0 | 100 | 0 | 17 |
| H. propinqua | A | 0 | 100 | 56 | 56 | 11 | 45 | 18 |
| | N | 100 | 0 | 4 | 0 | 96 | 0 | 28 |
| | G | 13 | 87 | 11 | 72 | 17 | 17 | 47 |
| | S | 100 | 0 | 12 | 0 | 88 | 0 | 16 |
| Cophosaurus | A | 0 | 100 | 73 | 73 | 0 | 18 | 22 |
| | N | 90 | 10 | 0 | 0 | 100 | 0 | 10 |
| | G | 44 | 56 | 25 | 13 | 60 | 19 | 16 |
| | S | 100 | 0 | 0 | 0 | 100 | 0 | 14 |
| Callisaurus | A | 0 | 100 | 50 | 40 | 10 | 20 | 10 |
| | N | 100 | 0 | 0 | 0 | 100 | 0 | 11 |
| | G | 20 | 80 | 80 | 0 | 20 | 60 | 5 |

S = submissive male; A = agonistic male; N = non-gravid female; G = gravid female

TABLE 3

COMPARISON OF BEHAVIORAL CHARACTERISTICS AMONG CERTAIN STATUS GROUPS OF LIZARDS*

| | | Placement | | Body | | Display | | Push-up | | Rapid Nod | | Attacked | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Moved | Remained | Flat | Raised | No | Yes | No | Yes | No | Yes | No | Yes |
| | S | X | | X | | X | | | X | X | | X | |
| H. lacerata | A | | | | | | | | | | | | |
| | N | | X | X | | X | | | X | X | | X | |
| | G | | X | | X | X | | | X | X | | X | |
| | S | X | | X | | X | | X | | X | | X | |
| H. maculata | A | | X | | X | | X | | X | | X | | X |
| | N | X | | X | | X | | X | | X | | X | |
| | G | | X | | X | | X | | X | | X | X | |
| | S | X | | X | | X | | X | | X | | X | |
| H. propinqua | A | | X | | X | | X | | X | | X | | X |
| | N | X | | X | | X | | X | | X | | X | |
| | G | | X | | X | | X | | X | | X | | X |
| | S | X | | X | | X | | X | | X | | X | |
| Cophosaurus | A | | X | | X | | X | | X | | X | | X |
| | N | X | | X | | X | | X | | X | | X | |
| | G | | X | | X | | X | | X | | X | | X |
| | S | X | | X | | X | | X | | X | | X | |
| Callisaurus | A | | X | | X | | X | | X | | X | | X |
| | N | X | | | X | X | | X | | X | | X | |
| | G | | X | | X | | X | | X | X | | | X |

S = submissive male; A = agonistic male; N = non-gravid female; G = gravid female

*Based on Table 2. X's indicate the activity of the major percentage of individuals in each category.

maintained in all of the species concerned, so that a generalization may be made concerning such behavior: the gravid females are aggressive, as are the agonistic males; the submissive males and non-gravid females share docile traits.

These behavioral characteristics may be the basis for sexual perception in these lizards. The reaction of a male to the response of an agonistic male or to a gravid female, which is aggressive, would be quite different from that encountered when he approaches a submissive male or a non-gravid female. In the former instance the stimulus is such that the male is challenged or rebuffed; in the latter case the situation creates an atmosphere of receptiveness and the male either courts or ignores the other lizard. In most cases, if the lizard approached is a submissive male, he will either run away at initial contact or move away very shortly thereafter. The role of the tail in posturing appears to have significance, for it was found to vary in attitude and movement both in species and sex. In H. lacerata, the tail was always raised and curled upward when the lizard was approached by another lizard. In every instance the gravid females waved the tail from side to side, but the submissive males and non-gravid females did so to a lesser extent. This particular tail curl and wave was quite characteristic of this species. A rapid switching of the tail just above the level of the substrate was the characteristic movement of submissive male and non-gravid H. maculata. On some occasions the tail was raised up, almost vertically, and held still. On most of the observations where a gravid female was concerned, the tail was not waved, although it was raised on almost half of the encounters. Most of the females of

H. propinqua raise the tail, although in a different manner. The switching of the tail of H. maculata is different from that of H. propinqua in that in H. maculata the whole tail is involved, whereas in H. propinqua only the distal half is waved. The tail of non-gravid females is usually rapidly waved; that of the gravid female almost never. In Cophosaurus the tail does not appear to have significance in sexual discrimination. Usually it is kept lowered and still upon an encounter, but the tail is frequently curled over the back and waved when individuals are moving about or asserting. There appears to be little difference between the sexes in this regard, however. The genus Callisaurus uses the tail extensively, and, upon encounter, the non-gravid female seems to curl the tail and wave it more than the lizards in the other genera.

The color of gravid females of the species studied appears to be of significance in sex recognition. A color change as obvious and typical of gravid lizards as the change in behavioral patterns occurs. In general, there is a suffision of a color into the dorsum which obscures the pattern, usually giving the lizard a uniform faded look. At the same time yellow or red or both appear as discrete spots or as bands of prominent color on the dewlap, sides of the body, the hind legs, or base of tail. The color, location, shape and extent of these chromatic markings vary with the species.

The acquisition of gravid color has been known for many years. Fitch (1956a) noted the appearance of red in the pattern of Crotaphytus, where the red is apparent as lateral spots. Van Denburgh (1922) called attention to pink coloration in Callisaurus females and Strecker (1915) described this coloration in Holbrookia texana (Cophosaurus). Strecker

(1910) mentioned that there is nuptial color in Holbrookia maculata and Smith (1943) mentioned the "pink color" in some specimens of the White Sands lizard, H. maculata ruthveni. Axtell and Wasserman (1953) noted the red color in H. propinqua, H. maculata, H. texana (=Cophosaurus), and Crotaphytus, and stated that only H. propinqua and H. maculata have red under the tail. In this study, red under the tail was noted only in H. propinqua, not in H. maculata. Axtell (1956) stated that the gravid female coloration of H. lacerata is greenish-yellow.

The coloration of gravid females of both Callisaurus and Cophosaurus is quite similar, but different from that of the other species studied. In both of these the dewlap is pink, and an orange-pink color line runs along the edges of the ventral surface of the body from the axillary to the inguinal region. This color bank is broad anteriorly and becomes abruptly more narrow at mid-body. Posteriorly, the band, if present, is quite narrow. No pink color is present on the posterior surface of the thighs nor on the undersurface of the tail.

In Holbrookia maculata the lateral band is narrow, but wider anteriorly than posteriorly. The color ranges from orange-pink to bright crimson. No color appears on the dewlap, but red spots may permeate the dorsal pattern until the normal pattern is obscured. In addition, a red stripe appears along the posterior surface of the thigh and may extend for a very short distance along the lateral base of the tail.

Holbrookia propinqua has the red stripe along the side of the ventral surface as in H. maculata. The posterior of the thigh also has a well-defined red stripe, best displayed at the lateral junction of the tail and thigh. The extension of red along the lateral base of the tail

is quite apparent. The underside of the tail is white at the base, but a short distance from the base an orange-red color appears, continuing (but fading) to the tip of the tail. This color may be deeper in some individuals than in others and it even extends onto the undersurface of regenerated tails.

Yellow also shows up in the coloration of gravid females. This is least apparent in Callisaurus and Cophosaurus.

In H. maculata and H. propinqua the cheeks become yellow; yellow appears along the sides of the body just above the red lateral stripe (this yellow is more noticeable in H. propinqua), and on the posterior of the thighs and adjacent lateral surfaces of the base of the tail. In addition, the light spots on the back of H. propinqua become yellow, whereas in H. maculata these spots may become yellow, pink-orange, pink, or red.

H. lacerata females develop only the yellow color. It covers the cheeks, sides of the neck, sides of the body, posterior of the thighs and the lateral base of the tail. The yellow suffuses throughout the entire dorsal pattern of the lizard. This yellow may have a greenish cast in some individuals.

The dorsal pattern of dark spots become obscured (or faded) in all of the species. The back of Callisaurus becomes a light blue-gray, Cophosaurus becomes either a light gray, blue-gray, blue, or brown. H. propinqua may be greenish-gray (very pale) or vary to greenish-brown with yellow spots. Red or yellow cause the dorsum of H. maculata to become quite uniformly light. H. lacerata is pale yellow to pale green-yellow. The loss of pattern is gradual, increasing until the most

extreme condition is present at the time of oviposition. A gradual increase in pattern and loss of yellow and red occurs after deposition of the eggs until typical non-gravid coloration is assumed.

In the various species these markings of red and yellow were noted to be intimately associated with specific posturings which caused these chromatic areas to be exhibited most emphatically to a courting male.

It also appears that olfactory cues were used at time to determine the species, sex, and perhaps the reproductive receptiveness of another lizard. "Tasting" of one lizard by another occurred frequently. The tongue was extruded and applied several times to various parts of the other lizard. Tasting was noted on the face, back of head, foreleg, and at various points along the side of the body.

Of more frequent occurrence was "cloacal nosing," in which one lizard approached another lizard from behind and pushed its snout beneath the base of the tail of the lizard being identified. It was not ascertained if the tongue was involved in this identification; it did not appear to be. Often a single nosing was sufficient, but at times there were repeated nuzzlings, occasionally with nudges of the snout. The recipient reacted in various ways, usually merely raising the tail and remaining still. Upon continued nuzzling or butting, the lizard might move away on tiptoe, it might stay in place, rise and wave the tail, or it might flatten and scoot along on its belly with the tail raised and waving rapidly.

Femoral pore secretions, which are most prominent in the male lizards during breeding season, were found by Hunsaker (1960) to be

distinctly different in amino acid composition in different species. He showed by experiment that the odor and taste produced by these secretions is species-specific and " . . . if other distinguishing marks are eliminated, lizards will associate with each other on the basis of this odor." Cloacal "nosing" may play a role, therefore, in species identification by olfactory cues produced by the femoral pores. It may also aid in identification of sex and receptiveness by olfactory means. Male lizards, in breeding condition and apparently sexually aroused, were noted on several occasions to press the cloacal region onto the substrate, flatten the thighs onto the surface, and drag the body along for short distances. This behavior would distribute spots of femoral pore secretion at various locations about the male's territory and could be a means of "signposting," a declaration of territory or an attractant to females. The trails made by cloacal dragging were observed on four occasions, but there appeared to be no obvious effect on other lizards crossing these trails. Males of H. propinqua, H. maculata, and H. texana were noted engaging in cloacal dragging.

# CHAPTER IV

# SOCIAL STRUCTURE

## Dominance

Social structure of iguanids has been studied by several investigators. Evans (1936) confined male Anolis carolinensis and found that a hierarchy of dominance was formed, with the largest lizard as the most dominant. Fitch (1940) noted that a dominant-subordinate relationship existed among Sceloporus occidentalis in the field. Schmidt (1935) noted territoriality in the marine iguana and found that females and young were tolerated, whereas males were driven away. A field study of Ctenosaura pectinata was conducted by Evans (1948) in which he found that a "tyrant" dominated the group of lizards, both males and females. The tyrant could move at will among the other lizards, but each of the lesser males was obliged to be confined to a small territory, with an indication of dominance among these males.

Evans (1935) found that Leiocephalus in captivity exhibited the dominant-subordinate relationship and that removal of the dominant resulted in a shuffle among the other males for dominant position. Carpenter (1961a, b) and Carpenter and Grubitz (1961) studied several genera of iguanids in captivity with results similar to the foregoing.

From these studies and others, it has become clear that within the family Iguanidae there is a general pattern of social behavior. Territories are established and guarded by males, who defend these territories by patrol, vigorous display, bluff, and combat. Females and submissive males are tolerated in this territory, but trespassing males are aggressively challenged. Under ordinary conditions, the males will be spatially separated, with few contacts between them, but when conditions force close crowding, a dominant-subordinate relationship is established, which may take the form of a dominance hierarchy.

In the present study, lizards were confined in outdoor enclosures in such numbers that contacts between individuals would be increased and numerous interactions could be noted. Males and females of each species were kept in the enclosures for varying lengths of time to note both the inter-and intra-specific interactions.

## Intraspecific Relationship

A general pattern was exhibited to which each of the species conformed. H. lacerata will not be considered because of the paucity of specimens.

When placed in the enclosure, the lizards spent some time examining their new surroundings, moving about and performing push-ups. Soon, it became apparent that there were some individuals more active than others. These individuals performed more push-ups and moved about more alertly.

The lizards began to show preferences for certain areas within the enclosure. In each of these groups one individual exhibited more activity than the others and moved about from one lookout point to

another, frequently doing push-ups. The other lizards in the group showed deference to this dominant lizard. When another lizard moved into the territory of this dominant, it was immediately challenged. If the newcomer ran away or assumed a submissive posture by flattening on the substrate, the dominant ceased display. If the trespasser returned the challenge, the two lizards sidled toward each other, laterally presented, doing occasional push-ups. In sidling, the lizard leaned toward his opponent and the hind leg on the adversary's side was dragged, the sidling approach being performed by the power of the hind leg on the opposite side.

When about three inches apart, the lizards stopped and remained motionless, sometimes for several minutes. The dominant usually initiated the next move by rushing in and grasping the invader in his jaws. The two lizards tumbled over until the hold was broken. The lizards assumed face-off positions and the display with push-ups was repeated, perhaps several times, or one of the lizards might dash in and grasp the other. Usually the interloper ran away after the initial tussle, but occasionally the dominant lizard was displaced.

Carpenter (1962a) tested response of Sceloporus undulatus to visual cues produced by others of the same species by placing a mirror in the enclosure in such a position that the lizard could see his image. Male Sceloporus postured at this "invader" in an aggressive manner.

In order to ascertain the effect of visual cues in the lizards under study, I placed an 8 X 10 inch mirror in the outdoor enclosure and in a 3 X 3 foot cage. Observations were made on both males and females of Cophosaurus, Callisaurus, and H. propinqua. The results for these

lizards were similar to those of Carpenter (op. cit.). Females of each species tended to ignore the image or move away from it. There was no indication of aggression. Submissive males usually moved away from the image. Dominant males, on the otherhand, upon seeing their image, began to posture and push-up toward it, with lateral presentation. As the movement of the lizard carried him beyond the edge of the mirror, he would cease posturing and appear to seek for the "other lizard." He would move around behind the mirror and appear excited. Upon coming in front of the mirror again, he would immediately assume the aggressive posture and sidle toward the "opponent" in full display. None of the lizards attacked the image, but several nudged at it. The length of time that such display continued varied. At times, the lizard moved past the edge of the mirror and continued on, not finding the image again. Other encounters lasted over ten minutes. The longer encounters terminated with the lizard appearing to tire of the stalemate and moving away slowly in partial display until the image was no longer in sight. This manner of retreat without submission was practiced by two individuals meeting in the enclosure when a stalemate occurred.

Four of the important features of aggressive behavior thus shown are similar to those expressed by Carpenter (1962a): (1) there is response by a male to another of his species, which is released upon visual cues; (2) response is conditioned by previous recent experience; (3) if challenge is made toward the image, it is stereotyped; and (4) active search may be instituted if the opponent (image) disappears.

Holbrookia exhibited aggregation into several separate groups, each group with one dominant. There was no single dominant for the

entire enclosure. When males from two separate territories met, either in an area between their territories or in the territory of one or the other, aggression was exhibited by one of the lizards. If each of the lizards was the dominant of his group, facing-off occurred, frequently ending with actual combat.

Cophosaurus and Callisaurus exhibited a single dominant for the entire enclosure. In this case, he exercised his dominance over individuals of both genera. There was little interaction between the dominant of either of these genera and individuals of Holbrookia.

Hyperaggression was exhibited by dominants of each species. At times the dominant lizard appeared to become unusually active, moving about, pushing-up frequently, and displaying, nudging, or attacking both males and females. These periods of hyperaggression often followed the attack and subsequent subjugation of a trespassing male by the dominant.

The determination of dominance by one male most often consisted of numerous aggressive displays toward the other lizards for only a day or two, after which there were few encounters in which the dominant was challenged. In some instances, however, the attainment of dominance by a single individual occurred only after a prolonged period of duels with one or more other aggressive males. An interesting illustration of this occurred in an enclosure in June, 1961. The outdoor enclosure measured 15 X 15 feet. It was provided with numerous piles of rocks and cement blocks for concealment and shade. The following lizards were placed into the enclosure on June 10: Cophosaurus, 10 males and 8 females; Callisaurus, 6 males and 8 females; and H. propinqua, 35 males and 35 females. It became apparent during the first day that one male Cophosaurus

was assuming dominance over most of the lizards in the enclosure. He moved about almost constantly, displaying and challenging. Almost all of his challenges were directed to other Cophosaurus and Callisaurus. The recipients were both males and females, which either ran away or flattened upon the substrate. One large Callisaurus male began to display and show aggressiveness to other lizards during the early afternoon. On the initial meeting of the dominant Cophosaurus and Callisaurus, each displayed at the other, facing-off laterally. The Cophosaurus did a push-up series and the Callisaurus moved away slightly. The Cophosaurus moved away in the opposite direction. This was the only interaction of the first day.

On June 11, the two met several times. The encounters were as on the previous day, but once the Callisaurus bit the Cophosaurus. Encounters on these two days between the two resulted in neither emerging victorious. Most of the activity of each was directed at other lizards, particularly after an encounter with each other. Cophosaurus appeared to have achieved dominance over Callisaurus by the morning of the following day. Cophosaurus ran at the other lizard almost every time that Callisaurus was in view. Callisaurus weakly displayed at Cophosaurus, curled his tail and ran away, frequently chased by Cophosaurus. Each of these males still displayed at other lizards during the day. Callisaurus was specially pugnacious toward smaller Callisaurus and, as evening approached, began to patrol the entire enclosure, displaying at other lizards. The dominant Cophosaurus ceased to attack him and once even flattened at display directed at him by the Callisaurus.

The Callisaurus was a definite tyrant on June 13. He moved about almost constantly challenging and biting other lizards. The Cophosaurus was challenged by him several times. On each occasion the Cophosaurus ran and attempted to escape up the side of the enclosure.

By the morning of June 15, the situation had reversed. The Cophosaurus chased the Callisaurus at every opportunity. Cophosaurus, thereafter, was the undisputed dominant. Although Callisaurus challenged and aggressively chased other Callisaurus and Cophosaurus, he never again challenged the authority of the dominant Cophosaurus.

In the ensuing days, the dominant Cophosaurus attacked and chased the Callisaurus at every opportunity. He seemed to have singled this lizard out for particular aggression. Other large male Cophosaurus were introduced into the enclosure, but they were promptly dominated and not picked on constantly. The attacks upon the Callisaurus became more and more severe, the Cophosaurus biting the Callisaurus in the side and on the legs. On June 30, the right front leg of Callisaurus was injured so badly that it could not be used. This lizard remained in hiding most of the time after this. It was removed to another enclosure on July 9, for it was becoming thin, and had lost half of the injured leg and most of the tail, presumably from aggression by the Cophosaurus on July 8.

The dominant Cophosaurus was removed from the enclosure on July 27. The Callisaurus was replaced in the enclosure on this date, as it had seemingly recovered from its injuries and emaciation. This lizard did not attempt to become aggressive toward other lizards.

The Cophosaurus was replaced in the enclosure on August 4. He immediately began to move about, displaying at all other lizards. When

he saw the Callisaurus, he attacked it with more vigor than his display at other lizards. He had returned and assumed dominance as if he had never been removed. His particular persecution of the single Callisaurus continued unremittingly, day after day. In a week, the Callisaurus had to be removed from the enclosure. It died soon after this removal. During the rein of this tyrannical Cophosaurus, this Callisaurus was the only lizard singled out for particular punishment. Other males and females were challenged, but not attacked.

This Cophosaurus was removed from the enclosure for 9 days in order to ascertain if another lizard would assume dominance in his absence. There was little difference in the social structure during this period. Some lizards moved onto his habitual basking spots, but there was no rise of another lizard into a dominant position.

Evans (1951) observed four males and two females of Cophosaurus in a terrarium for twenty days during the period January 15 and March 16, 1950. He found that one male had assumed dominance within three days by intimidating. When this dominant was removed, another male took "possession," but became subordinate to the first when it was returned. When both of these lizards were removed, a third male became dominant over the remaining male and females.

No evidence of the rise of a new dominant appeared in the present study of 1961. This may be attributed to the short length of time that the dominant was removed. The other lizards had become so conditioned to the pattern of subordination that more time may have been needed to release them. Also, the time of the year may have played a role. In the late summer the territorial drive may not be as evident as in early spring.

Removal of the dominant was repeated again in the summer of 1962. The lizards of the previous summer had died, except for one male. This was Cophosaurus (C. t. 4). When placed in the outdoor enclosure with other recently collected lizards on May 3, he quickly began to assert and, by the next day, had assumed dominance. All of the lizards were removed from the enclosure on May 29. On June 11, five male and four female Cophosaurus were placed in the enclosure. C. t. 4 was not one of these. Male C. t. 5 began to assert almost immediately. This lizard had been completely subordinate to C. t. 4 when the two were together previously and he even had been bitten and chased by a much smaller male H. maculata. This lizard was larger than C. t. 4 but had been submissive. Now, released from the subjugation imposed by C. t. 4, he was assuming a dominant role in the enclosure. By the next day, he had succeeded in intimidating the other lizards and he moved about, actively asserting.

Cophosaurus C. t. 4 was placed in the enclosure on June 16. Soon after his arrival, he began rapid nodding at a female. This attracted the attention of the more recent dominant, C. t. 5, which came rushing down at C. t. 4. The two presented laterally for a moment; then C. t. 4 fled and was chased by C. t. 5. Each time that C. t. 4 was placed in the open, he would either run from C. t. 5 or assume a prostrate submissive posture. Male C. t. 4 was removed from the enclosure. Male Cophosaurus C. t. 5 retained control of the dominant position until he was removed from the enclosure on July 2.

At the time of removal of the dominant C. t. 5, there were six male Cophosaurus present in the enclosure, all submissive to this

male. Within three days, male C. t. 24 had risen to dominance. He held this position until July 30. On this date, both of the earlier dominants, C. t. 4 and 5, were placed in the enclosure. The former dominant C. t. 5 achieved a dominant position by intimidation after two days, but C. t. 4 was dominated by several males other than C. t. 5. Number 24, continued to challenge C. t. 5, but retreated from each encounter during the remaining days of observation. Table 4 gives the interactions between the Cophosaurus males from July 30 through August 15. It shows that a dominance hierarchy existed among these males. Males C. t. 26 and 30 had few encounters due to the secretiveness resulting from their low social status.

Callisaurus were not placed in an enclosure alone, but during the summer of 1961 were in an outdoor enclosure which also contained Cophosaurus and H. propinqua. No hierarchy was exhibited by the Callisaurus, but there was considerable interaction between Cophosaurus and Callisaurus and, to a less extent, between Callisaurus and H. propinqua. Individuals of Callisaurus were subjugated by the dominant Cophosaurus. Two of the Callisaurus exhibited dominance over other Callisaurus. One of these dominant Callisaurus (C. d. 6) exercised dominance over three Cophosaurus, but was in turn dominated by Cophosaurus C. t. 1. The interactions between the Callisaurus and Cophosaurus are shown in Table 5.

H. maculata were tested for territoriality and dominance by placing four males and four females into the outdoor enclosure for the period June 12 through July 23, 1962. Definite preference for certain areas within the enclosure was exhibited, but there appeared to be a lack

TABLE 4

SOCIAL STATUS OF ENCLOSED GROUP OF COPHOSAURUS TEXANUS. RESULTS OF ENCOUNTERS DURING PERIOD JULY 30 THROUGH AUGUST 15, 1962

| Subordinate (loser) Lizard Code Number | Dominant (winner) Lizard Code Number | | | | | | | | Total Subordinate Encounters | Total All Encounters | Size | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 5 | 24 | 4 | 27 | 1 | 26 | 22 | 30 | | | Length (mm) | Weight (g) |
| 5 | | | | | | | | | 0 | 16 | 73 | 11.4 |
| 24 | 5 | | | | | | | | 5 | 14 | 63 | 8.9 |
| 4 | 2 | 2 | | | | 1 | | | 5 | 9 | 61 | 8.3 |
| 27 | 2 | 2 | 2 | | | | | | 6 | 7 | 64 | 8.2 |
| 1 | 3 | 2 | | | | | | | 5 | 6 | 56 | 6.5 |
| 26 | 2 | | | | 1 | | | | 3 | 4 | 73 | 13.3 |
| 22 | 1 | 3 | 2 | 1 | | | | | 7 | 7 | 64 | 8.4 |
| 30 | 1 | | | | | | | | 1 | 1 | 59 | 7.0 |
| Total Dominant Encounters | 16 | 9 | 4 | 1 | 1 | 1 | 0 | 0 | | | | |

TABLE 5

SOCIAL STATUS OF ENCLOSED GROUP OF *CALLISAURUS DRACONOIDES* AND *COPHOSAURUS TEXANUS*.
RESULTS OF ENCOUNTERS DURING PERIOD JUNE 10 THROUGH AUGUST 4, 1961

| Subordinate (loser) Lizard Code Number | | Dominant (winner) Lizard Code Number | | | | | | | | | | | | | Total Subordinate Encounters | Total All Encounters | Size | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Callisaurus | | | | | | | | | Cophosaurus | | | | | | Length (mm) | Weight (g) |
| | | 6 | 25 | 20 | 1 | 15 | 3 | 21 | 9 | 5 | 11 | 3 | 7 | 1 | | | | |
| Callisaurus | 6 | | | | | | | | | | | | | 32 | 32 | 47 | 78.6 | 10.7 |
| | 25 | | | | | | | | | | | | | | 0 | 3 | 66.8 | 7.8 |
| | 20 | 5 | 1 | | | | | | | | | | | 4 | 10 | 10 | 62.0 | 6.2 |
| | 1 | | | | | | | | | | | | | 1 | 1 | 1 | 73.9 | 10.6 |
| | 15 | 2 | | | | | | | | | | | | 1 | 3 | 3 | 55.0 | 5.2 |
| | 3 | 1 | | | | | | | | | | | | 1 | 2 | 2 | 63.4 | 6.6 |
| | 21 | | | | | | | | | | | | | 1 | 1 | 1 | 68.7 | 8.6 |
| | 9 | 1 | 2 | | | | | | | | | | | 1 | 4 | 4 | 65.0 | 6.2 |
| | 5 | | | | | | | | | | 1 | | | | 1 | 1 | 72.2 | 8.4 |
| Cophosaurus | 11 | | | | | | | | | | | | | | 0 | 1 | 62.0 | 8.8 |
| | 3 | 1 | | | | | | | | | | | | | 1 | 1 | 62.9 | 7.3 |
| | 7 | 1 | | | | | | | | | | | | | 1 | 1 | 71.0 | 10.9 |
| | 1 | 4 | | | | | | | | | | | | | 4 | 45 | 65.0 | 8.5 |
| Total Dominant Encounters | | 15 | 3 | | | | | | | | 1 | | | 41 | | | | |

of pugnacity in the lizards. In the infrequent encounters which resulted in display, one lizard (H. m. 4) dominated each of the others. There was no interaction among the other male lizards. This dominant H. m. 4 did not patrol the entire enclosure, as did the dominant Cophosaurus or Callisaurus, but spent almost all of the time on one side of the enclosure.

H. propinqua males not only exhibited territoriality, but also a dominance hierarchy both within the territories and among the dominants of each of the territories.

Twenty-three male H. propinqua were observed in social interactions in the outdoor enclosure during the summer of 1961. After an initial period of acclimation to the new environment, each lizard appeared to become a habitue of a particular area. Four of these areas became evident: the northeast corner, the east side and southeast corner, the southwest corner, and a central clear area. Each area was separated from the other by grasses or cement blocks, although there were several connecting open paths. Thus, there were four fairly stable aggregations of H. propinqua. Individuals from one area frequently moved temporarily to or through one of the other areas, causing challenge from the dominant of the trespassed area and perhaps challenge from other males as well. One male was the obvious dominant in each area, with an indistinct hierarchy of dominance among the other males. Table 6 lists the encounters occurring among the four most active males from each area.

In the summer of 1962, an attempt was made to ascertain dominance and territoriality in H. propinqua in the outdoor enclosure. They were observed from July 4 through July 23. These lizards were the same lizards used the previous summer. Preferential areas of the

TABLE 6

SOCIAL STATUS OF ENCLOSED POPULATION OF HOLBROOKIA PROPINQUA DURING PERIOD JUNE 10 THROUGH AUGUST 4, 1961. ENCOUNTERS BETWEEN MALES FROM VARIOUS TERRITORIES

| Subordinate (loser) Lizard Code Number | TERRITORY | | | | | | | | | | | | Total Subordinate Encounters | Total All Encounters | Size | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | E-SE | | | | NE | | | | SW | | | | CENTER | | | | | | | |
| | Dominant (winner) Lizard Code Number | | | | | | | | | | | | | | | | | | Length (mm) | Weight (g) |
| | 97 | 18 | 58 | 80 | 48 | 61 | 82 | 52 | 47 | 7 | 26 | 56 | 81 | 5 | 28 | 87 | | | | |
| 97 | | | | | 1 | | | | | 1 | | | 1 | | | | 3 | 16 | 56.7 | 4.5 |
| 18 | 1 | | | | | | | | 2 | 1 | | | 1 | | | | 5 | 11 | 59.8 | 4.8 |
| 58 | | | | | | 1 | | | | | | | 1 | | | | 2 | 7 | 57.4 | 4.9 |
| 80 | 2 | 1 | 1 | | 1 | | | | | | | | 1 | | | | 6 | 12 | 49.0 | 3.7 |
| 48 | | | 1 | | | | | | | | | | | | | | 1 | 24 | 53.7 | 4.4 |
| 61 | | 1 | 1 | | | | | | | | | | | | | | 2 | 7 | 53.5 | 4.1 |
| 82 | | | 1 | | 2 | | | 1 | | | | | 2 | | | | 6 | 7 | 58.3 | 4.8 |
| 52 | 1 | | | 1 | | | | | | | | | | | | | 2 | 3 | 52.8 | 3.9 |
| 47 | | | | | | | | | | | | | | | | | 0 | 8 | 54.9 | 4.5 |
| 7 | 3 | | | 2 | 2 | 1 | | | 4 | | | | 3 | | 2 | | 17 | 23 | 54.7 | 5.2 |
| 26 | | | | | | 1 | 1 | | 1 | | | | | | | | 3 | 4 | 52.9 | 5.1 |
| 56 | 1 | | | | | | | | | | | | | 1 | | | 2 | 2 | 47.3 | 3.5 |
| 81 | 1 | 3 | 1 | | 11 | 1 | | | 1 | | 1 | | | | | | 19 | 42 | 54.2 | 4.3 |
| 5 | 4 | 1 | | 1 | 3 | 1 | | | | 2 | | | 5 | | | | 17 | 19 | 57.0 | 4.4 |
| 28 | | | | | 3 | | | | | 2 | | | 1 | | | | 6 | 8 | 53.0 | 4.3 |
| 87 | | | 1 | | | | | | | | | | 2 | 1 | | | 4 | 4 | 47.0 | 3.3 |
| Total Dominant Encounters | 13 | 6 | 6 | 4 | 23 | 5 | 1 | 1 | 8 | 6 | 1 | 0 | 17 | 2 | 2 | 0 | | | | |

enclosure were noted after the first day. The lizards generally basked in the same area, but later moved to separate areas for the remainder of the day. Most of the lizards moved about a great deal, but there were surprisingly few interactions. Table 7 shows the interactions which were observed. One lizard, H. p. 61, dominated all of the others, but did not patrol the entire enclosure. Most of the interactions appeared incidental to his general moving about, rather than as part of regular territorial pursuits. This lizard was defeated once when it wandered into the southeast corner, which was within the territory of another male. The males, other than the dominant, exhibited no definite hierarchy. It appeared to be somewhat territorial, but there were insufficient encounters for this to be definitely determined.

Size of the individual appears to play a major role in dominance. This has been borne out in the studies of others on various iguanid species (Carpenter, 1961a, b; 1962b; Fitch, 1940, 1956a; Evans, 1935, 1936, 1938a). In my study the dominant lizard of each of the species was not the largest of the individuals present, either in length or weight, but was larger than most of the lizards of its species. The difference between the dominant and the larger, but subordinate, lizards appeared to be amount of activity, rather than size alone. Occasionally, a much smaller, but more active, lizard could cause a larger lizard to retreat.

## Territoriality

The concept of territoriality is basic to a study of social structure in animals. Many studies have shown that territoriality is exhibited by numerous species of vertebrates. Territories function in

TABLE 7

SOCIAL STATUS OF ENCLOSED GROUP OF HOLBROOKIA PROPINQUA. RESULTS OF ENCOUNTERS DURING PERIOD JULY 4 THROUGH JULY 23, 1962

| Subordinate (loser) Lizard Code Number | Dominant (winner) Lizard Code Number | | | | | Total Subordinate Encounters | Total All Encounters | Size | |
|---|---|---|---|---|---|---|---|---|---|
| | 7 | 81 | 11 | 10 | 61 | | | Length (mm) | Weight (g) |
| 7 | | | 1 | 1 | 3 | 5 | 8 | 56.2 | 4.3 |
| 81 | | | 1 | | 3 | 4 | 6 | 58.0 | 6.1 |
| 11 | 1 | 1 | | | 5 | 7 | 9 | 52.3 | 4.1 |
| 10 | 1 | 1 | | | 3 | 5 | 6 | 52.6 | 4.6 |
| 61 | 1 | | | | | 1 | 15 | 55.4 | 4.3 |
| Total Dominant Encounters | 3 | 2 | 2 | 1 | 14 | | | | |

distributing individuals over the available habitat in order that the carrying capacity is not exceeded. In addition, the territory furnishes a retreat where reproductive activities may proceed undisturbed.

Iguanid lizards were previously known to exhibit territoriality. Numerous genera within the family have been studied in this respect (Evans, 1938a, 1948, 1953; Fitch, 1940, 1956a; Carpenter, 1961a, b; Norris, 1953; Noble and Bradley, 1933; Schmidt, 1935). The genus Phrynosoma appears to be the exception, as no territoriality was noted by Lynn (1963).

Cagle (1950) stated that H. texana (Cophosaurus) appeared to select a home range. An individual which was disturbed moved from one to another of a few selected sites. Milstead (1959) secured data from drift-fence trapping of the same species which indicated possible home range behavior. The longest recorded movement of any individual was 175 feet.

Gates (1957), studied the herpetofauna of an area in Arizona. He agreed with Tevis (1944) that the individual range for Callisaurus has an axis of approximately 50 feet.

Recapture data by Milstead (1961) indicated that the home range for male H. maculata was 0.169 acre and for the female 0.181. He defined the "home range" as that area in which the lizard is usually active, as distinguished from the "home realm," all of the area in which the lizard is normally active from day to day.

In nature, the territorial male lizards are spread over the available habitat and contact other males infrequently. When environmental conditions become changed, however, so that crowding of the males

occurs, interactions between males are more frequent. This leads to the formation of a dominance hierarchy or an autocracy. In the experimental enclosures, both forms of social relationships among the males were evident. Territoriality was indicated in each of the forms studied. Males tolerated other males within the bounds of their territory only if the other males were subordinate. The choice basking and resting spots were not used by subordinate males, but the dominant male tolerated females upon these sites. Often, however, the male displayed at these females and moved them away.

Subordinate males in the genera Cophosaurus and Callisaurus remained away from the vicinity of the dominant male, but in the Holbrookia species, groups of males stayed together along with certain females, each group dominated by a single male. Each of these groups was separated from the others as a territorial unit.

Cophosaurus and Callisaurus exhibited similar territorial behavior in 1961 by a single dominant male patrolling the entire enclosure. No minor territories were established by subordinate males. On the other hand, H. propinqua established small territories controlled by a single dominant male, but containing males and females. Each of the lizards moved about into the territories of other lizards, where aggressive interactions occurred. Table 6 shows the territorial design of 16 H. propinqua in 1961.

In 1962, observations on enclosed groups of Cophosaurus, H. propinqua, and H. maculata indicated that the territorial patterns noted the previous year were established again, and that an obvious difference existed between the patterns of Cophosaurus and Holbrookia.

A diagram of the enclosure is given in Fig. 13, with the entire area divided for purposes of analysis as shown. The early morning sun, shining upon areas 3 and 6, the rock piles and log, made these favorite basking areas. Most lizards were found in these areas early in the morning, but moved to other preferred areas of the enclosure after initial basking.

Observations upon Cophosaurus indicated that areas were selected by dominance. The dominant male moved from one favorite spot to another through the day, patrolling at frequent intervals. The places chosen as lookouts and resting stations were raised positions, such as the log and rock piles. These same areas were preferred by the females. The subordinate males utilized these places only in the absence of the dominant male. Areas which were frequented by the individual Cophosaurus are shown in Fig. 14. It may be noted that the areas of utilization are discrete for the males, whereas the females use mutual areas, shared with the dominant male. The association of these lizards is shown in Table 8. This table gives the percentage of times two individuals were observed together in relation to total observations. The dominant male Cophosaurus (C. t. 5) was intolerant of the presence of other males, and none were observed with him. The other males were infrequently observed together, but each generally stayed in an area segregated from the others. Number 1 male, was a young male, smaller and more active than the other males, except for the dominant. He frequently moved about, and was the only male to utilize any of the dominant's lookout points. Females were most frequently observed associated with the dominant male, but occasionally with each of the

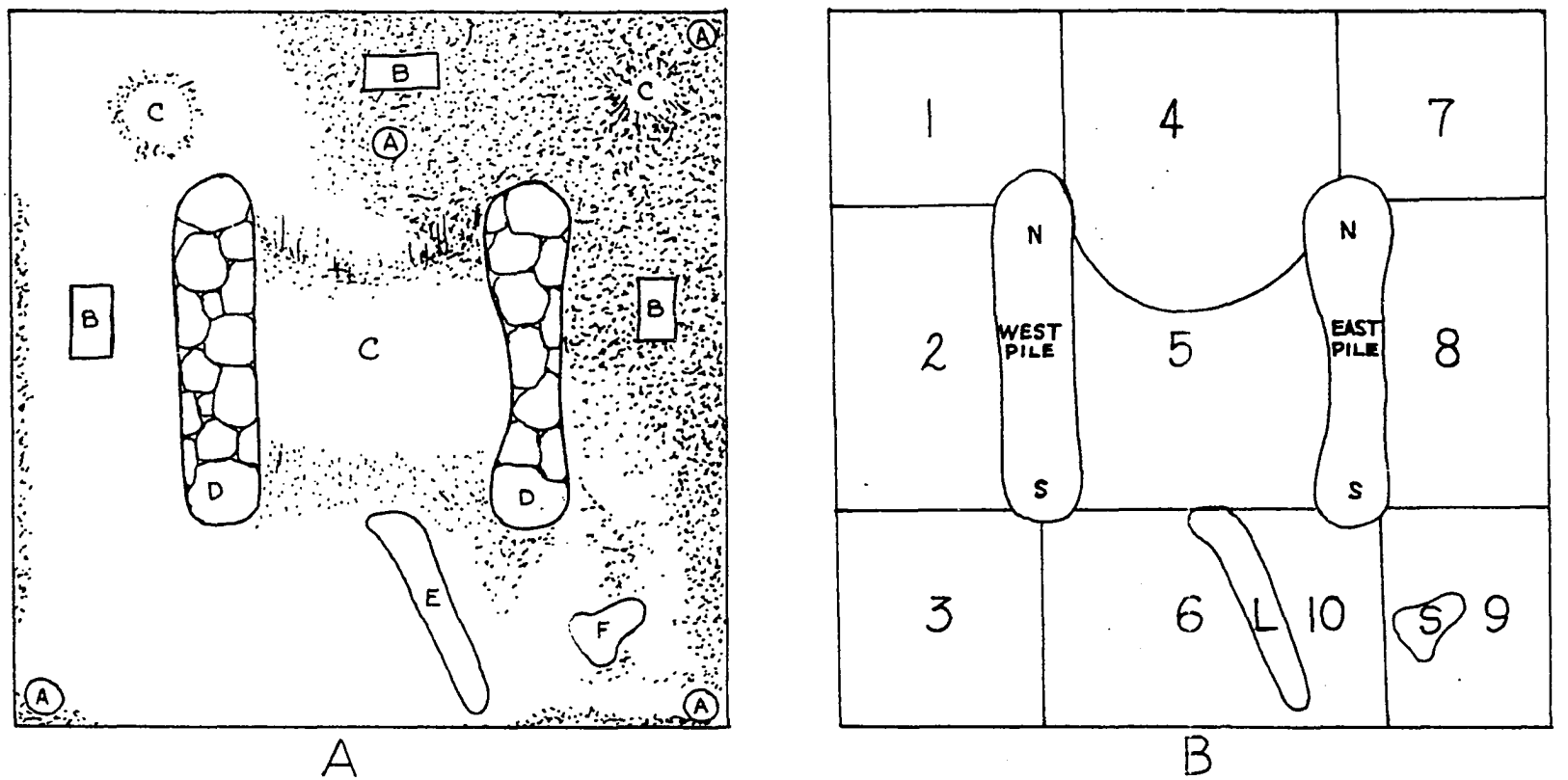



Fig. 13. A. Diagram of 15 X 15 feet outdoor enclosure used during the summer of 1962 for observation of lizards. Letters represent the following: A. drinking dishes, B. wooden shade shelters, C. sand hills, D. rock piles, E. log, F. stump. Stippled areas represent grass.
B. Hypothetical division of enclosure for purpose of analysis of lizards' movements.

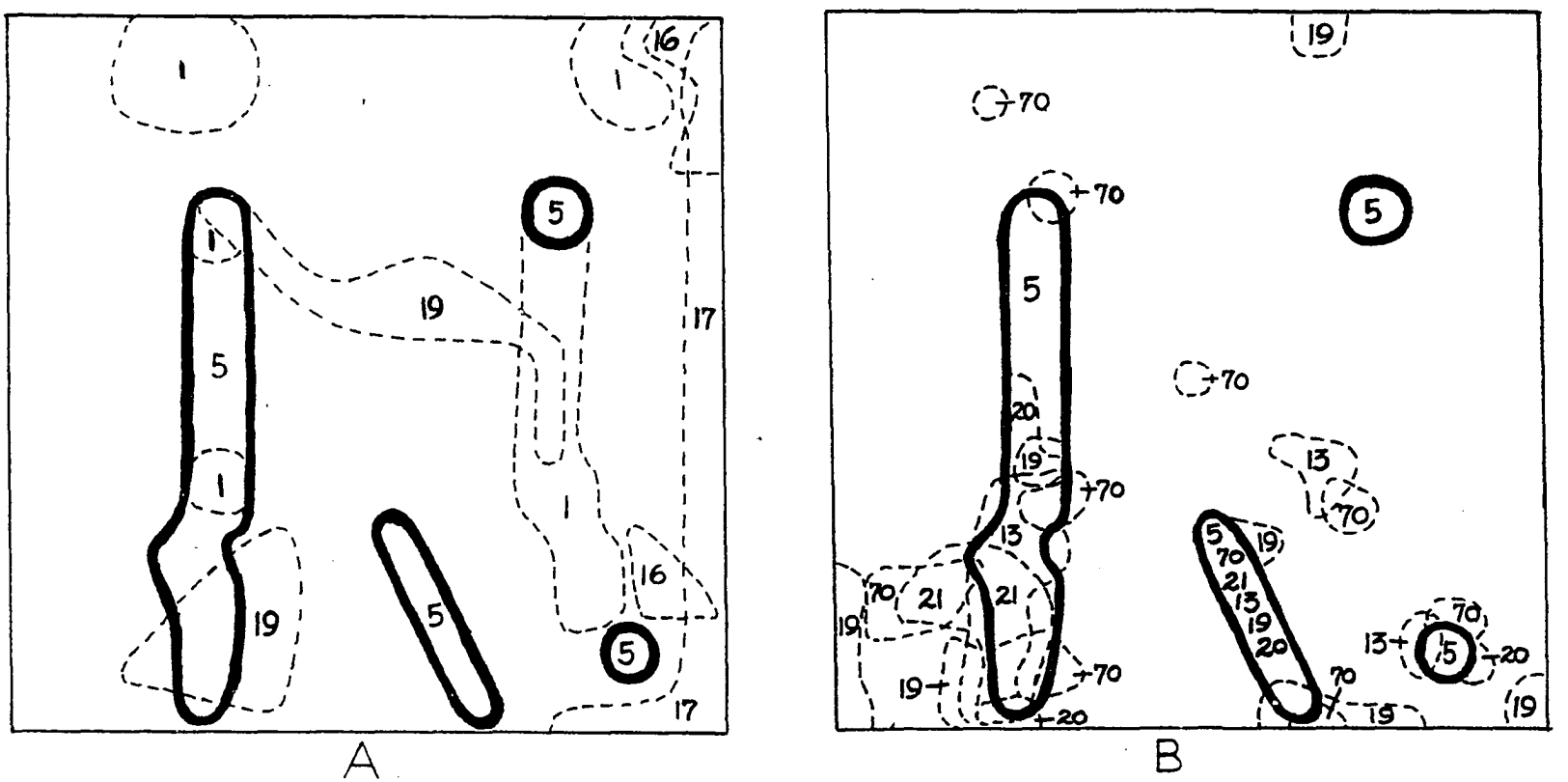



Fig. 14. Areas of utilization in enclosure by individuals of Cophosaurus texanus. A represents areas of five males. B represents areas of five females. In both diagrams the areas of the dominant male are outlined heavily. Numbers represent the identification number assigned individual lizards.

TABLE 8

ASSOCIATION OF INDIVIDUALS OF *COPHOSAURUS TEXANUS*, PERCENTAGE OF TIMES OBSERVED TOGETHER IN 62 OBSERVATIONS

| | Lizard Code Number | Females | | | | | Males | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 20 | 70 | 19 | 13 | 21 | 19 | 8 | 16 | 1 | 5 |
| Males | 5 | 11.1 | 22.6 | 6.5 | 8.1 | 24.2 | | | | | |
| | 1 | 2.8 | | 4.9 | 4.9 | 1.6 | 1.6 | 3.2 | 1.6 | | |
| | 16 | | | 3.2 | | | 4.9 | 8.0 | | | |
| | 8 | | | 4.9 | 3.2 | | | | | | |
| | 19 | 2.8 | 4.9 | | | 4.9 | | | | | |
| Females | 21 | 19.5 | 25.8 | 14.5 | 25.8 | | | | | | |
| | 13 | 11.1 | 12.9 | 12.9 | | | | | | | |
| | 19 | 8.3 | 6.5 | | | | | | | | |
| | 70 | 5.6 | | | | | | | | | |
| | 20 | | | | | | | | | | |

subordinate males. The table shows the high degrees of association among the females, indicating that segregated territoriality was expressed by the males and not by the females.

Five males and two females of H. propinqua were observed in the enclosure. Although the aggressive interactions noted indicated that one male, H. p. 61, was dominant over each of the other males, this dominance was not expressed as a territorial right to the exclusion of other males. Table 9 shows the association between individuals. It will be noted that there is association among individuals of the same sex and between sexes. Selected areas of the enclosure were preferred, but there was a large amount of overlap. The preferred areas are shown in Fig. 15. Aggressive interactions indicate that males do defend certain areas at times, but are tolerant of other males at other times, particularly morning basking.

Four males and four females of H. maculata were observed in the enclosure in 1962. The results of these observations were similar to the observations upon H. propinqua. More overlap of preferred areas existed (Fig. 16) than in either H. propinqua or Cophosaurus, and there appeared to be no definite dominant established for a particular area. The segregation of the H. m. 1 female, shown in Fig. 16, is due to advanced gravidness, at such times females of Holbrookia often isolated themselves. This behavior was not noted in gravid female Cophosaurus or Callisaurus.

Association among individuals of H. maculata is given in Table 10. No individual appeared to be segregated from other individuals, each having been observed associated with each of the others. The pattern

TABLE 9

ASSOCIATION OF INDIVIDUALS OF HOLBROOKIA PROPINQUA, PERCENTAGE OF TIMES OBSERVED TOGETHER IN 60 OBSERVATIONS

| | Lizard Code Number | Females 80 | Females 73 | Males 61 | Males 10 | Males 11 | Males 88 | Males 7 |
|---|---|---|---|---|---|---|---|---|
| Males | 7 | 3.3 | 8.3 | 1.7 | 5.0 | 1.7 | 5.0 | |
| Males | 88 | 8.3 | 26.7 | 21.7 | 6.7 | 11.6 | | |
| Males | 11 | 5.0 | 8.3 | 8.3 | 8.3 | | | |
| Males | 10 | 6.7 | 11.6 | 6.7 | | | | |
| Males | 61 | 11.6 | 18.4 | | | | | |
| Females | 73 | 13.3 | | | | | | |
| Females | 80 | | | | | | | |

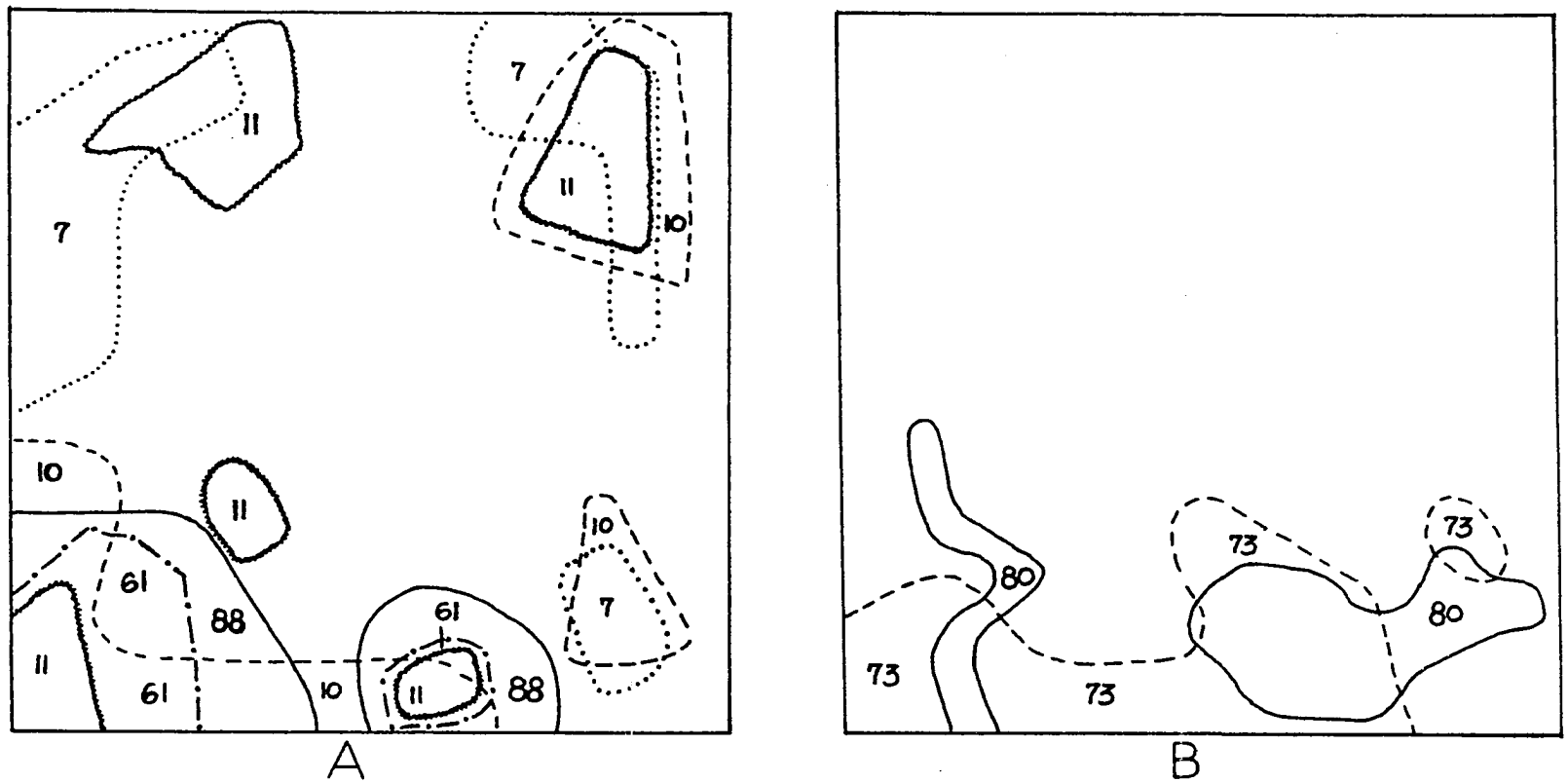



Fig. 15. Areas of utilization in enclosure by individuals of Holbrookia propinqua. A represents areas of five males. B represents areas of two females. Numbers represent the identification number assigned individual lizards.

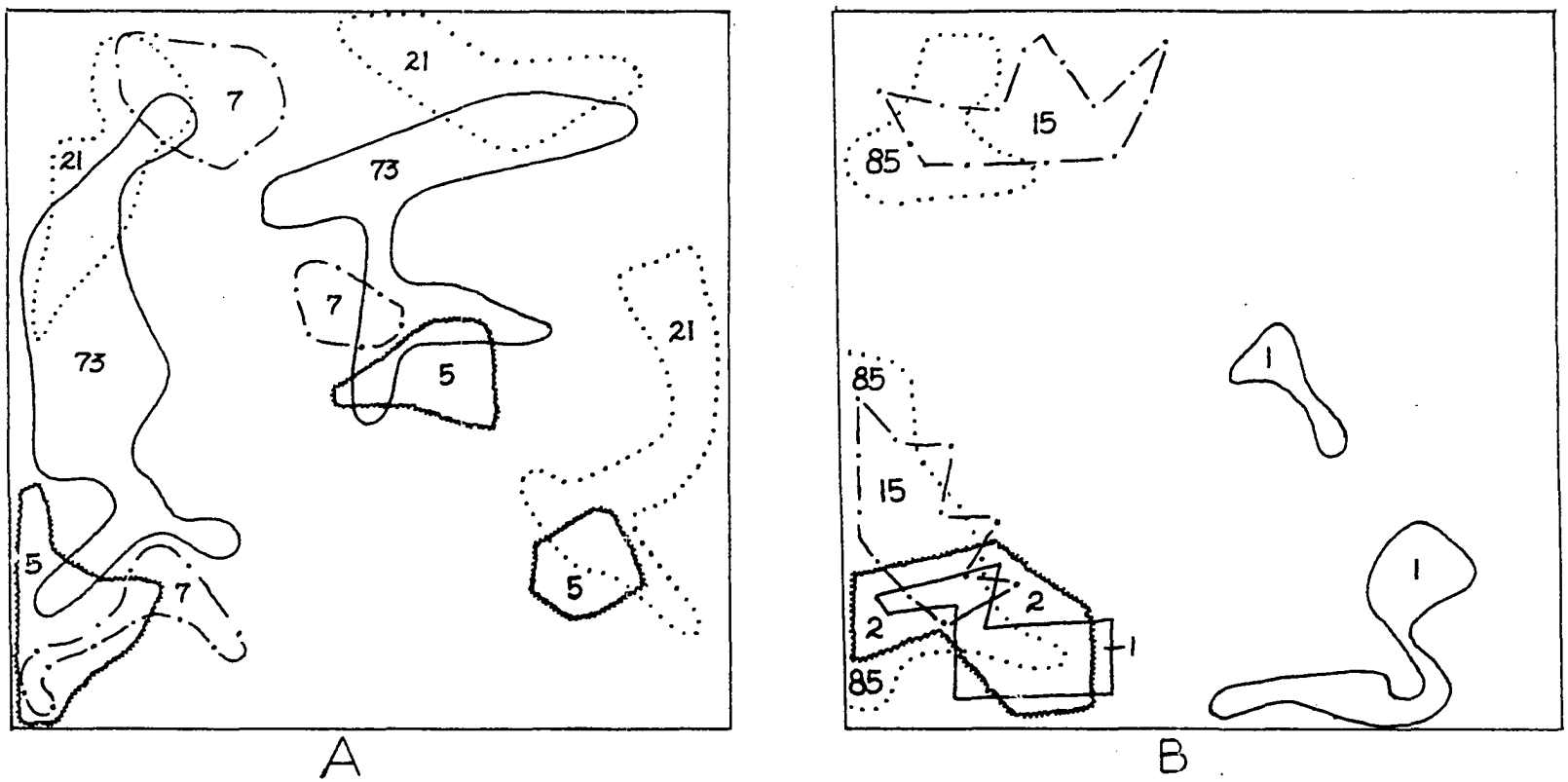



Fig. 16. Areas of utilization in enclosure by individuals of Holbrookia maculata. A represents areas for four males. B Represents areas for four females. Numbers represent the identification number assigned individual lizards.

TABLE 10

ASSOCIATION OF INDIVIDUALS OF HOLBROOKIA MACULATA, PERCENTAGE OF TIMES OBSERVED TOGETHER IN 62 OBSERVATIONS

| Lizard Code Number | | Females | | | | Males | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 77 | 1 | 2 | 15 | 21 | 73 | 4 | 7 |
| Males | 7 | 8.1 | 8.1 | 12.9 | 12.9 | 6.5 | 14.5 | 11.3 | |
| | 4 | 11.3 | 17.8 | 21.0 | 11.3 | 3.2 | 6.5 | | |
| | 73 | 9.7 | 4.8 | 9.7 | 12.9 | 12.9 | | | |
| | 21 | 12.9 | 3.2 | 8.1 | 4.8 | | | | |
| Females | 15 | 11.3 | 9.7 | 14.5 | | | | | |
| | 2 | 14.5 | 9.7 | | | | | | |
| | 1 | 3.2 | | | | | | | |
| | 77 | | | | | | | | |

of association seems to be one of individuals moving about over the area with a minimum of hostility exhibited.

Differences in territorial behavior patterns may be correlated with conditions of populations of these species found in the field. Cophosaurus and Callisaurus are frequently abundant in their natural habitats but are usually found as segregated individuals, each male separated from any others by an obvious gap. Both Holbrookia maculata and H. propinqua, are found most frequently in rather dense population clusters, individuals often only a few feet apart. Often, too, the requirements for habitat niche are more restricted for Holbrookia than for Cophosaurus or Callisaurus, the physical environment forcing closer grouping of individuals, with reduction of individual territories and increased areas of overlap. The reduction of territorial behavior, with increased tolerance for other individuals, would allow more individuals to occupy available habitat, provided that the carrying capacity is not exceeded.

# CHAPTER V

# TEMPERATURE AND PERIODICITY

## Temperature

Lizards depend upon insolation and substrate radiation to bring their body temperature to a level sufficient for functional efficiency. Cowles and Bogert (1944) showed that many lizards are able to maintain their body temperatures within a narrow range by means of behavior. Later, Bogert (1949) showed that the preferred body temperatures within closely related species are similar, but differ from temperatures preferred by other groups. Temperature preferences have been examined in iguanids by Norris (1953), Fitch, (1956a, b), Blair (1960), and Carpenter (1961c). These studies support the contention of Bogert as to specificity of temperature preference. It is also shown by these authors that the preferred body temperature is rather high (32-38°C), and approaches closely the critical maximum.

The role of various environmental factors in thermoregulation has been examined by several investigators. Weese (1917), Cole (1943), Cowles and Bogert (1944), and Mayhew (1963) pointed out that the substrate temperature is the most important body temperature determining factor when there is lack of solar radiation and that air temperature is found to have minor influence on the temperature of the lizard. Soule' (1963), however,

recently studied thermoregulation in nine species of lizards from Baja California and found a definite correlation between air temperature and body temperature. Cole (1943) pointed out, also, that increase in body temperature of lizards was only slightly influenced by metabolic or muscular activity.

Behavioral thermoregulatory studies cited previously have been confined for the most part to the movements of lizards into and out of the sun, to times of diel activities, and to other phases of periodicity. Few descriptions of thermoregulatory posturing have appeared in reports.

Cloacal temperatures of lizards in the enclosure were taken from June 23 through August 26, 1962. In all, 389 temperatures were recorded. These temperatures were taken at various times of the day, under differing weather conditions, and of lizards in various thermoregulatory postures. Temperatures were recorded also of the substrate at the point where the lizard was taken and of the air 2 cm. above this point. All cloacal temperatures were obtained using a Schultheis quick-registering mercury thermometer. The thermometer was placed into the cloaca of the lizard within ten seconds of capture, and the lizard was held so that a minimum amount of the captor's hand was in contact with the lizard. Ambient temperatures were taken with the thermometer bulb shaded. In addition to the cloacal temperatures taken during this period, temperatures were recorded at time of capture of lizards taken on field trips. Thirty-three records were available for H. maculata and Callisaurus, and eight records for Cophosaurus. No field records were available for H. lacerata or H. propinqua.

Table 11 shows the temperatures of the lizards which were taken in the enclosure on clear days between the hours 9:00 A. M. and 5:00 P. M. This was the period when the sun was shining into the enclosure. During this period the lizards had the opportunity to select a "preferred" body temperature, for a thermal gradient was present in the form of sun and shade. The mean of the temperatures for each species was considered to be the preferred body temperature (PBT).

Mayhew (1963) studied thermoregulation in Sceloporus orcutti. He utilized cloacal temperatures taken of all lizards active in the open, regardless of the time of day. The upper 50 per cent of the temperatures taken were considered to constitute the "preferred activity range" (PAR). This range of temperatures is that within which the lizards were most active. Table 11 shows the PAR for lizards in my study. The PAR is quite high in each of the species, near the critical maximum. The PAR is narrow in Cophosaurus and Callisaurus; broader in Holbrookia. H. maculata shows the broadest PAR. This species ranges more northward than the others, and the wide PAR is indicative of this broader geographic range.

Table 12 gives the PBT as a mean of cloacal temperatures taken of lizards as they were captured in the field. These temperatures differ somewhat from the PBT given in Table 11. In the case of Callisaurus and Cophosaurus some of the temperatures were taken during cloudy weather. The PBT for H. maculata is a bit higher than in Table 11 because all of these were actively moving about in the sun, whereas none were noted while they were basking as a prelude to activity. Only two temperatures were taken of H. lacerata in the field, both on a cloudy, cool day. One,

TABLE 11

CLOACAL TEMPERATURES OF LIZARDS IN ENCLOSURE BETWEEN 9:00 A. M. AND 5:00 P. M. DURING PERIOD JUNE 23 THROUGH AUGUST 26, 1962

| | Mean Temperature (PBT) °C | Range °C | Preferred Activity Range* (PAR) °C | Number of Temperatures Taken |
|---|---|---|---|---|
| H. maculata | 35.7 | 27.4 - 40.8 | 33.2 - 40.8 | 41 |
| H. propinqua | 37.8 | 31.0 - 40.4 | 37.0 - 40.4 | 45 |
| H. lacerata | 38.1 | 30.8 - 42.5 | 37.3 - 42.5 | 22 |
| Cophosaurus | 38.3 | 31.8 - 40.9 | 38.1 - 40.9 | 60 |
| Callisaurus | 39.2 | 34.2 - 41.6 | 39.0 - 41.6 | 20 |

*PAR represents the upper 50 per cent of all temperatures taken.

TABLE 12

CLOACAL TEMPERATURES OF LIZARDS AT TIME OF CAPTURE IN THE FIELD

| | Mean Temperature (PBT) °C | Range °C | Number of Temperatures Taken |
|---|---|---|---|
| H. maculata | 37.5 | 31.0 - 42.2 | 33 |
| Cophosaurus | 37.0 | 33.6 - 41.5 | 8 |
| Callisaurus | 38.1 | 31.8 - 41.4 | 33 |

for the male, was 32.8°C, and the other, a female, was 28.5°C. No temperatures were taken of H. propinqua, for each lizard was captured only after a frantic chase across the open sand dunes.

The preferred temperatures of the lizard species studied is a reflection of both ecological and geographic factors. Each of the lizards is an inhabitant of open areas, where vegetation is scant. In these areas temperatures are generally high. Species which live in wooded areas would be in an environment where temperatures would be somewhat lower. Sceloporus is a tree or rock dweller and, as a genus, is usually associated with vegetated areas, although some species have invaded more open regions. The PBT of various species of Sceloporus has been found to be from 32.9°C to 36.9°C (Bogert, 1949). Mayhew (1963) gave 32.6°C as the PBT for S. orcutti, Carpenter (1960) gave 34°-35°C for S. undulatus, and Bogert (1959) gives 34°C for "many species from various environments." Fitch (1956b) lists 39°-40°C for Cnemidophorus and Carpenter (1960) gives 38°C as the PBT for this genus. Cnemidophorus is an active diurnal lizard of open areas. In the Iguanidae, those lizards characteristic of open regions exhibit high PBT also. Fitch (1956a) gives 37° to 40°C for Crotaphytus, and Cowles and Bogert (1944) list the following PBT for desert species: Gambelia, 38.7°; Dipsosaurus, 37.4°; Sauromalus, 37.7°; Uma, 38.3°; and Phrynosoma platyrhinos, 36.8°. Thus, the higher PBT is noted in those forms which are typically found in desert regions. The lizard genera of the present study indicate their relationship with the other desert iguanids by their high PBT.

Geographically, the PBT is an expression of range. Callisaurus is found on the low desert flats of the southwest where the highest

temperatures prevail. It has the highest PBT of any of the lizards in the present study. Cophosaurus is typically southwestern, but is more widespread and found in rocky areas, where the temperature may be lower on occasion. It has a lower PBT than Callisaurus, but the close relationship is evident. H. lacerata occurs in much the same situation as Cophosaurus, but is more restricted geographically. It has a PBT quite close to that of Cophosaurus. H. propinqua is restricted to southeastern Texas in open sandy dunes, but the temperature is mitigated by the proximity of the Gulf of Mexico. H. maculata, as stated before, has a broader range than the other species, occurring much farther to the north. It, too, often inhabits grasslands. The lower PBT, as an adaptation to cooler habitats, has probably enabled this form to become more widespread.

## Color Change

Atsatt (1939) studied the color change of desert iguanids. She found that low temperature caused darkening and high temperatures caused lightening in the color pattern. This reaction to temperature was noted by me in each of the lizard species studied, but was most marked in Callisaurus, Cophosaurus, and H. lacerata. When first emerging the lizards were very dark in color, but as the body temperature entered the preferred activity range, the color lightened, until it was lightest near the critical maximum temperature.

Of the lizards which I studied, Atsatt observed only Callisaurus critically, and Cophosaurus to a lesser extent. It was found by her that Callisaurus entered the light phase around 40°C. It differed from all

other iguanids studied by exhibiting a second light phase at continued low temperatures of about 20°C.

Color change has the thermoregulatory function of increased heat absorption during the dark phase, when the lizard's body temperature is low, and decreased heat absorption during the light phase, when little increase in body temperature is desired.

## Postures

The usual posture of all of the sand lizards when the body temperature has reached the optimum temperature range is an attentive stance with the head raised, the forelegs partly flexed, holding the chest well off of the substrate, and with the pelvic region in contact with the substrate. The orientation of the body may or may not be related to the position of the sun.

When the body temperature of the lizard is below the optimum range or when the ambient temperatures are extreme, the postures of the lizard deviate from that described above.

In the early morning or late in the evening, the temperature of the substrate is greater than that of the air but both are lower than the optimum range of the lizard (Fig. 17). At these times the lizard flattens on the substrate with the entire undersurface of the body and chin in contact with it. Also, the legs are spread in such a way to place their maximum area in contact with the substrate (Fig. 18A). The long axis of the body of the lizard is usually oriented so that maximum surface is exposed to the sun's rays. The lizard may lie on an incline of the substrate which would place the long axis of the body at right

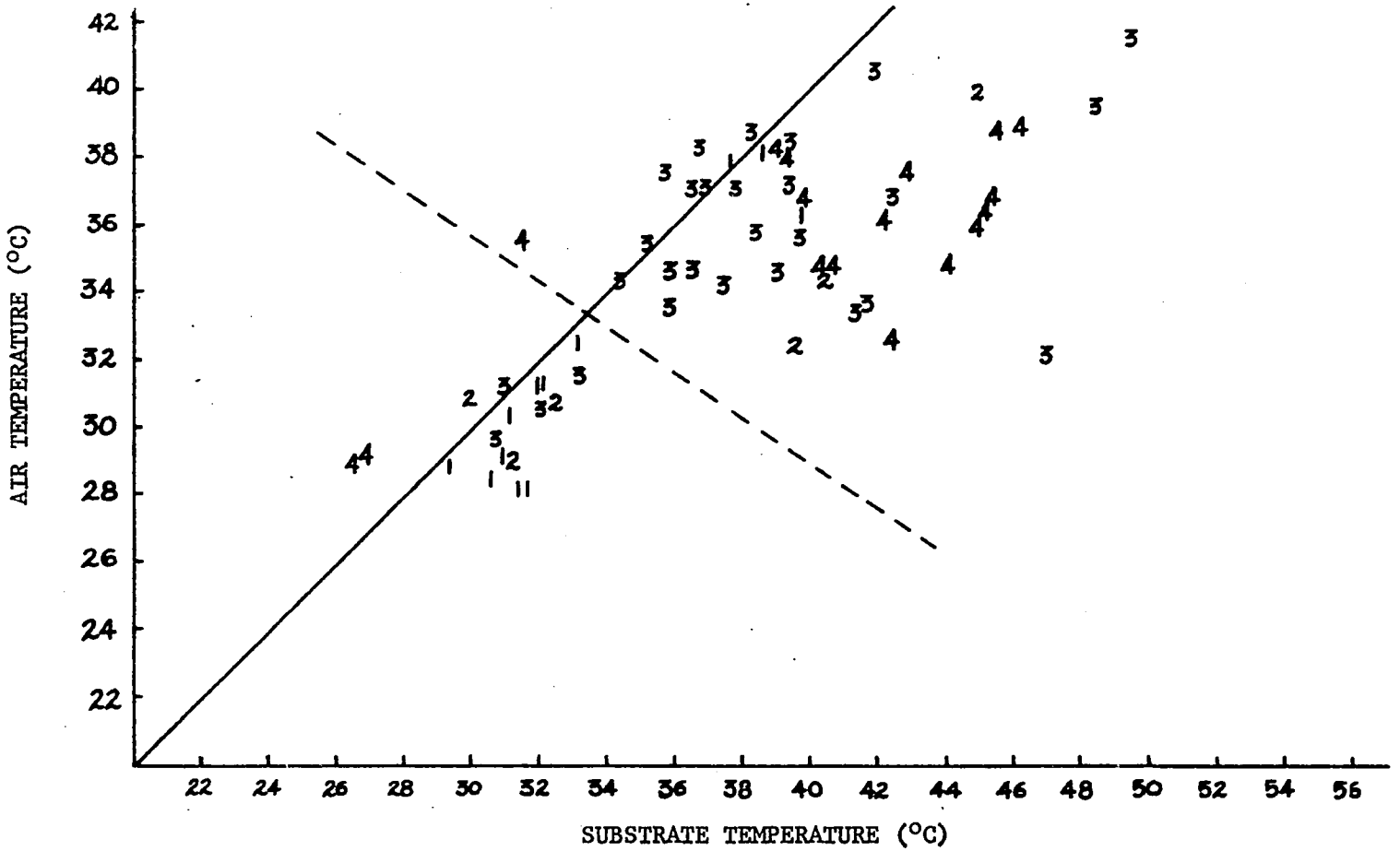



Fig. 17. Comparison of postures in low and high cloacal temperature groups in relation to air and substrate temperatures. Points below dashed line represent cloacal temperatures in the 29 - 30°C group; above dashed line in the 38 - 40°C group. Numbers represent posture of the lizard: 1. flattened; 2. belly down, head up; 3. cloaca down, chest up; 4. body completely elevated.




Fig. 18. Thermoregulatory postures: A. lizard flattened on substrate, B. body of lizard tilted in order to achieve right angle orientation to the sun's rays, C. same result achieved by lizard climbing onto slanting rock.

angle to the rays of the sun. At times, the body may be tilted in order to achieve this right angle orientation (Fig. 18B, C).

The lizard may be in the open at times when the substrate temperature is quite above the optimum range of the lizard. The posture of the lizard then is one in which minimum body surface is in contact with the substrate. The legs are extended, raising the entire body, and the tail may be elevated also (Fig. 19A). The soles of the feet appear to be quite sensitive to temperature increase. When the substrate is hot, the toes curl upward, leaving the heel alone in contact with the substrate (Fig. 19B, C). At this time the body is held high, also. The lizard usually does not stay in such a place for long. Sometimes, the toes of the front feet are not curled upward, but the soles of the feet are raised, the tips of the claws alone contacting the substrate.

Carpenter (1961c) observed toe-raising in Cnemidophorus. He proposed that this might be a thermoregulatory behavior pattern for cooling the lizard, since the vascular toes offer a proportionally greater surface area than other parts of the body.

Axtell (1960) reported females of H. maculata climbing into weeds and grasses when the ground temperature became too warm. These lizards then oriented themselves so that the long axis of the body was parallel to the rays of the sun. The lizard illustrated by Axtell was a gravid female. In the present study, gravid females of H. maculata and H. lacerata as well as both males and non-gravid females of H. maculata and H. propinqua and males of H. lacerata were noted behaving in this way. Not only did lizards climb into vegetation to orient themselves parallel to the sun's rays, but they frequently achieved this orientation by placing their forefeet upon a raised object.

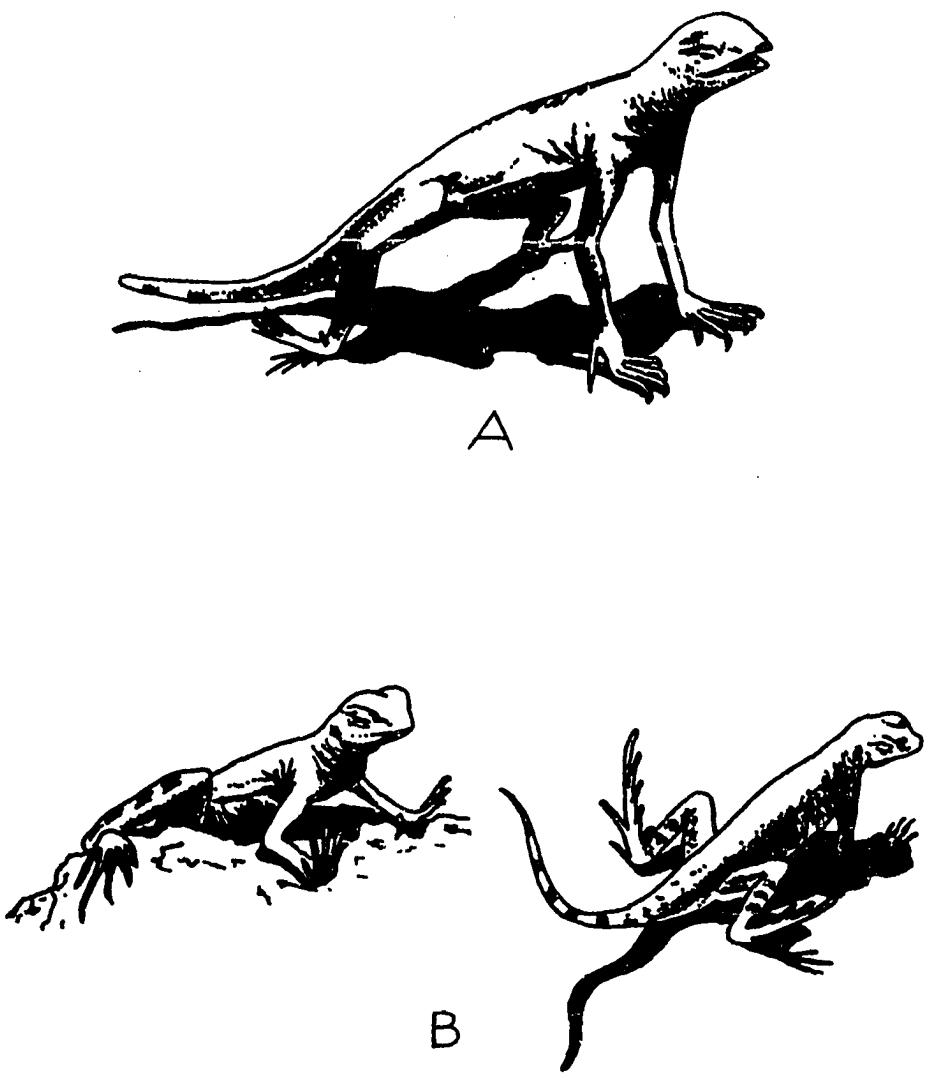



Fig. 19. Thermoregulatory postures: A. position assumed when the lizard's body temperature is near the maximum voluntary tolerance and the substrate temperature exceeds the body temperature, B. method of toe-lifting when the substrate is hot.

By presenting as little body surface as possible to the sun's rays, the lizard is able to reduce the amount of radiant energy absorbed and, thus, to keep increase in body temperature to a minimum. When the substrate temperatures are extremely high, the temperature of the air only a few inches above the substrate may be considerably lower. This would account for the lizard climbing into the grass.

Four stations were set up in the enclosure for the period July 5 through July 15, 1962, in order to ascertain changes in air temperature and various substrate temperatures during the course of the day.

A thermistor thermometer was used to monitor the temperatures, the probes placed in such a manner that they were shaded from the direct rays of the sun and secured so that their position would not vary. The air probe was placed 2 cm. above the surface of the sand, and a probe placed just below the sand's surface. A probe was placed on the surface of a small log and one on the surface of a large sandstone rock. Both the log and the rock were utilized by the lizards as basking and observation posts.

Temperatures were recorded hourly or more often during the period of study. Notes were made on lizard posture and other behavior and cloacal temperatures were taken of lizards at various times of the day. Air temperatures were taken at one meter above the ground, the thermometer shaded by the observer's body. Most of the days were clear and hot, but partly cloudy, completely cloudy, and rainy conditions also occurred.

Temperatures of air and substrates for this period are presented in Fig. 20 as means for each hour. Before the sun began to shine into the enclosure, the temperatures were all nearly alike. Soon, the temperatures began to increase rapidly, with the rock temperature lagging behind. The sun began to shine into the enclosure about 8:30 A. M. From this time there was an extremely rapid rise in all temperatures, but the rate of increase was more for each substrate than for air. The air temperature became near maximum between 11:00 A. M. and noon, but the sand and log temperatures did not peak until 1:00 P.M. The rock temperature continued to increase until 3:00 P.M. At this time all of the temperatures began to decrease, the sand and log more rapidly than the rock and air. The sun ceased to shine into the enclosure at about 5:00 P. M. At this time the air, log, and rock temperatures were almost the same, all being higher than the air temperature. After 5:00 P. M. the rock temperature remained higher than any of the other temperatures. At 7:30 P. M. all of the temperatures were approximately the same, but three or four degrees above those of 7:30 A. M. The maximum temperatures for the sand and log were between 54° and 56°C; for the rock, 48° to 50°C; and for the air about 42°C. The activity of the lizards followed closely the changes in temperature of the substrates and air. Thermoregulatory posturing was dependent also upon these temperatures. As the lizards first emerged in the morning, their body temperatures were that of the sand in which they were buried. This was generally between 26° and 28°C. The lizards moved into a spot of sun on the sand or log and flattened their body so that a maximum amount of the undersurface was in contact with the substrate. Insolation warmed the lizards above the temperature

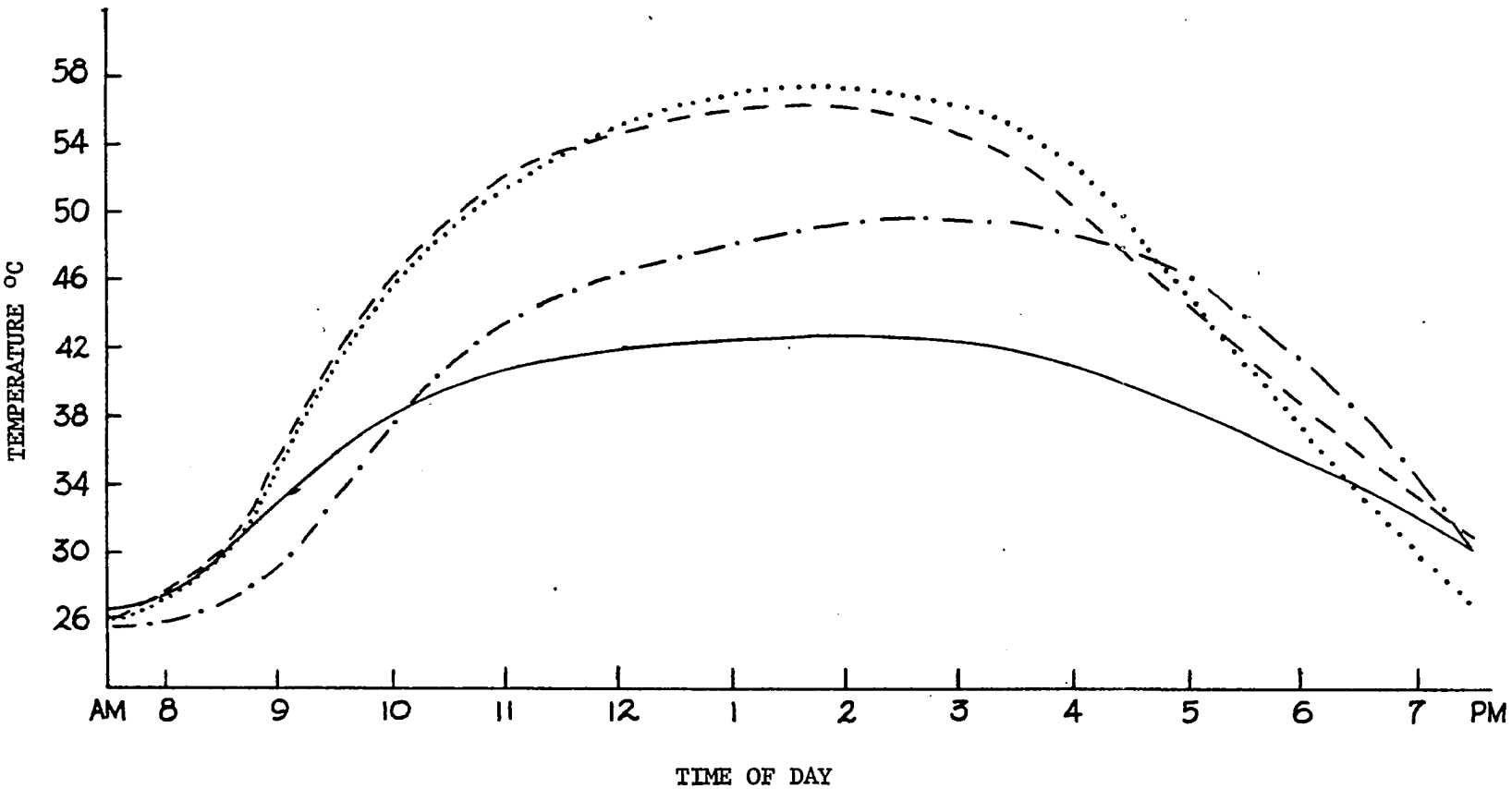



Fig. 20. Hourly mean temperatures of air and substrates in enclosure during the period July 5 through July 15, 1962. Air (2 cm above substrate), solid line; sand, dotted line; log, dashed line; rock, dash-dot line.

of the substrate and they raised the fore parts of their bodies, assuming the "alert" posture. Those lizards which were on the rocks in the sun before 10:00 A. M. were either flattened or raised somewhat, depending upon the relation of the air temperature, rock temperature, and wind. If the rock temperature was near that of the air and a breeze was blowing, the lizards would flatten out upon the rock surface. Early in the basking period this posture was preferred because a maximum amount of body surface was exposed to the sun and heating was more rapid.

A period of usual activity prevailed from the time that the lizards achieved a body temperature within the preferred activity range until the substrate and air temperatures became so high that it was necessary for the lizards to seek shelter. On the graph (Fig. 20) it can be noted that after 9:00 A. M. the log and sand surfaces exposed to the sun were at the maximum level of tolerance for any of the species. From this time on, the lizards did not stay on these exposed surfaces for long and, when posturing, held their bodies somewhat raised from the substrate. The rock surface did not achieve this level until between 10:30 and 11:00 A. M. Until this time, lizards were noted on the rocks, many in flattened postures.

During the period 9:00 to 12:00 A. M., lizards moved actively about from sun to shade and across sunny spots and areas of dappled light. In general, after 11:00 A. M. the temperatures of the substrates in the sun and the air were above the maximum tolerance and activity was conducted in shaded spots. Most of the lizards had sought shelter by this time and remained there with little movement.

The high temperatures persisted until about 3:00 P. M., when lizards began to move about again in shade and sun.

After 5:00 P. M., when the sand, log, and air temperatures were decreasing rapidly, many lizards first began assuming thermoregulatory postures on the log and sand in the sun. Soon, however, the temperature of these approached the lower limits of the preferred activity range of the species and the lizards either burrowed into the sand for the night or climbed upon the rocks and flattened. After 6:00 P. M., the sand and log temperatures dropped, and the lizards were flattened upon the rocks. Here they remained until the falling temperature of the rock and the failing light of day caused them to retire for the night.

Figs. 21 and 22 show the relationship of the body temperatures of the lizards to the air and substrate temperatures. The body temperatures follow closely the ambient temperatures until they reach 30° to 32°C. The air and substrate temperatures are closely associated until they reach this temperature, which corresponds with 8:30 A. M. in Fig. 20. The body temperatures of the lizards exceed the air and substrate temperatures above this point, indicating that the temperatures of the lizards are raised through insolation. Only at the highest air temperatures, 38° to 42°C, do these values exceed the body temperature of the lizard, and then only in a relatively few instances. The substrate temperature exceeds the body temperature of the lizard when the substrate is above 40°C. The disparity between the cloacal temperature of the lizard and either the air or substrate temperature when these are above 32°C indicates that the lizard is using other means for regulating its temperature and that it is not dependent upon a single ambient temperature when

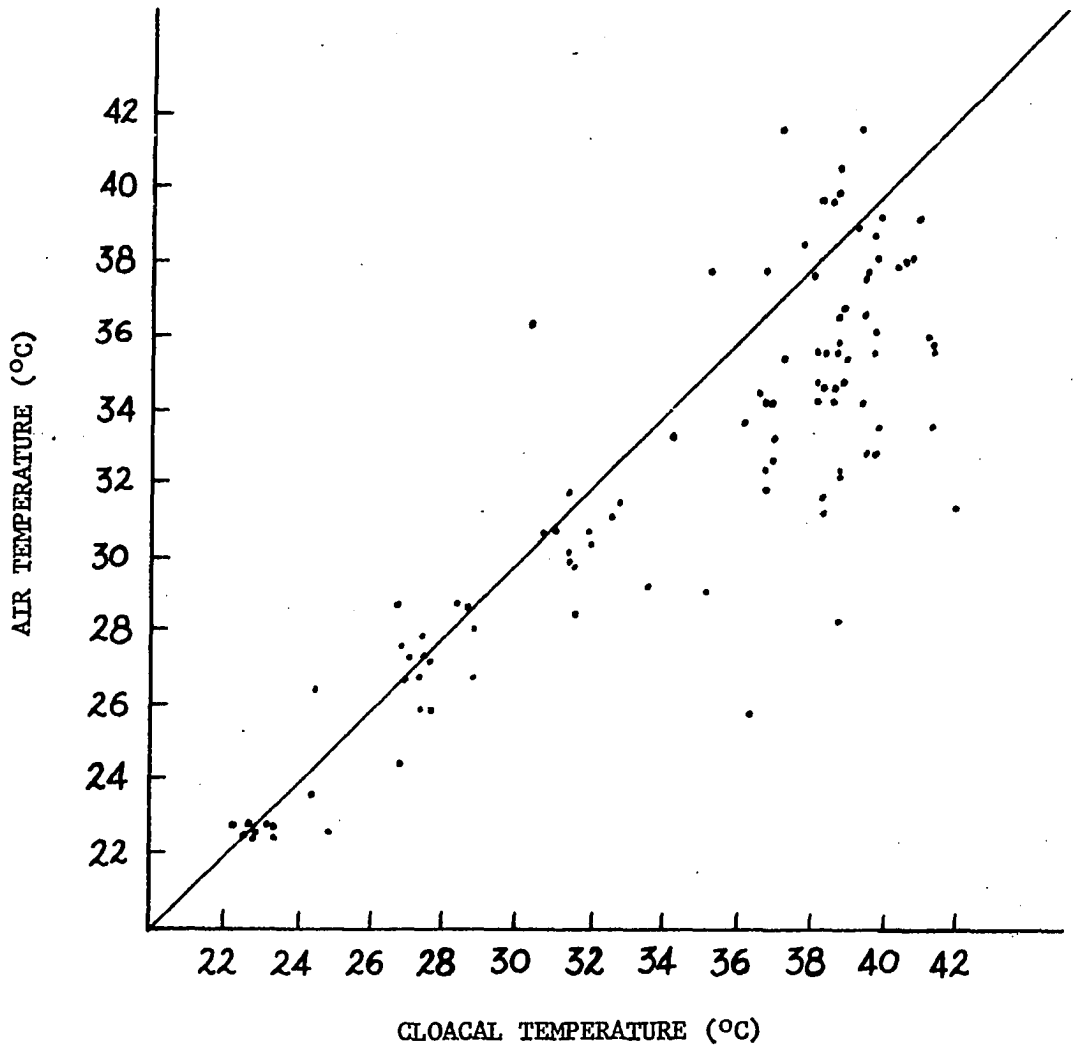



Fig. 21. Scattergram of 101 cloacal temperatures of all species studied in relation to the air temperatures recorded 2 cm above the substrate.

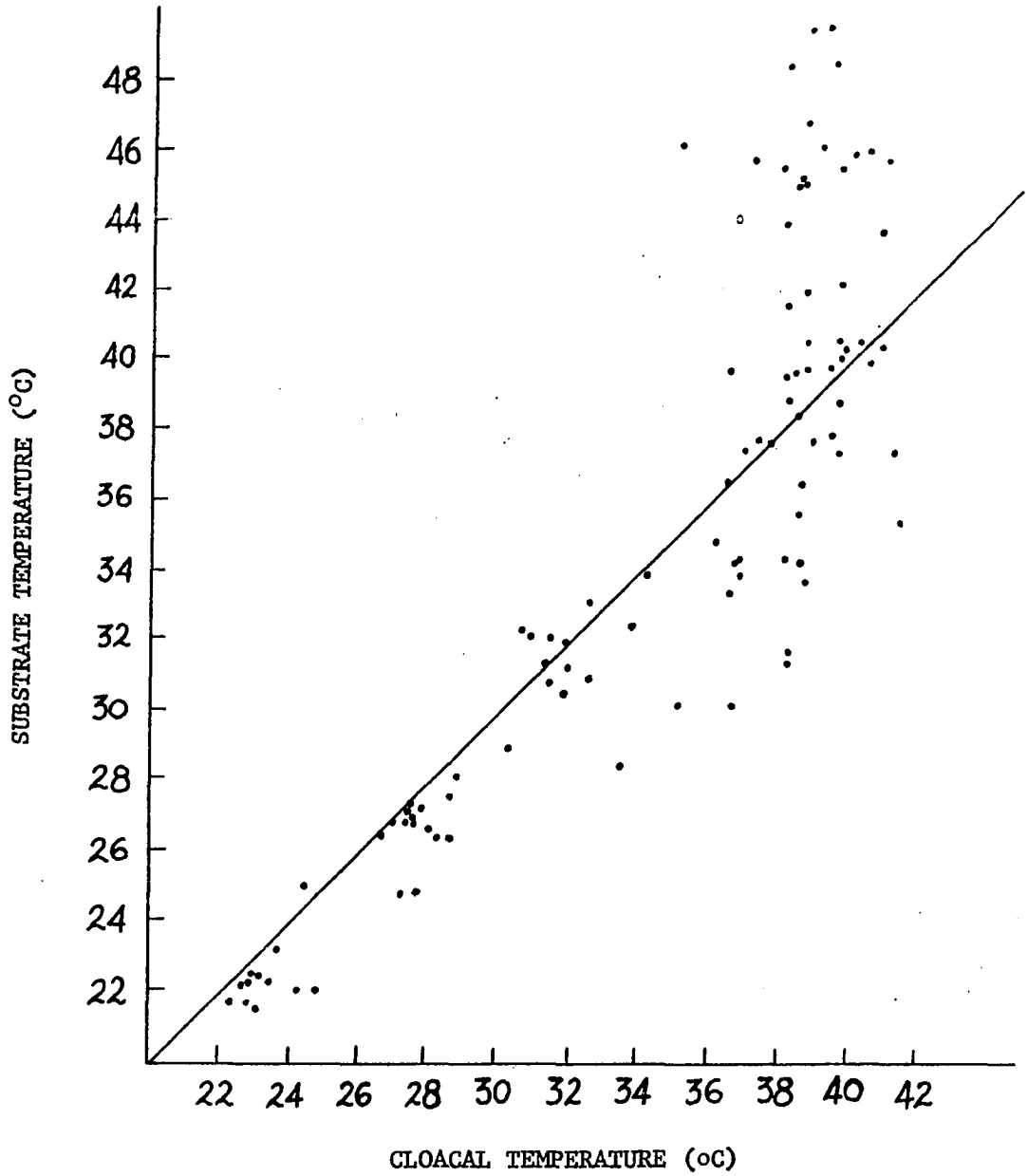



Fig. 22. Scattergram of 101 cloacal temperatures of all species studied in relation to the substrate temperatures.

a minimal value is exceeded. By behavioral posturing, the lizard can utilize the air temperature, substrate temperature, and insolation in wuch a way as to keep its body temperature within the narrow range of temperatures at which it can function best.

Fig. 17 shows postures of lizards in relation to both air and substrate temperatures. At lower temperatures, the lizards may flatten if the air and substrate temperatures are alike, but will raise from the substrate if the air temperature exceeds the substrate. At higher temperatures, more usual postures are maintained, but if the substrate is near the upper limit or exceeds the maximum tolerance of the lizards, the lizards hold their bodies well above the surface of the substrate where the air temperature is considerably lower. If the substrate temperature is below the minimum of the activity range of the lizards but the air temperature is within this range, the lizards hold their bodies up away from the substrate.

Those lizards whose body temperatures were near the critical maximum often added respiratory cooling to posturing in order to prevent further increase in body temperature. The lizards stood with their legs extended, bodies held high above the substrate, and remained for long periods with their mouths open. This occurred when both air and substrate temperatures were at or above the critical maximum. Although shade was available, many of these lizards remained, facing into the sun, for prolonged periods. Cowles and Bogert (1944) called attention to the fact that lizards do possess the ability to dissipate heat through rapid respiration and that it is most effective in dry regions. Desert reptiles, however, can ill afford to utilize this device because of the water loss involved.

## Periodicity

In temperate climates, ectothermic animals exhibit an annual cycle in which a period of winter hibernation or quiescence alternates with a period of warm weather activity. In those United States lizards which occur near the Mexican border, the winter period of inactivity may be brief and interrupted by many periods of activity on warmer days. Ransey (1948, 1949) described hibernation of Cophosaurus in Texas. The intermittent nature of this hibernation is evidenced by the fact that he found some of the lizards fairly active on February 17, 1949.

Little is known of the dates of entering and emerging from hibernation in any of the lizards studied. The only species to occur in Oklahoma, H. maculata, first emerged on April 15, 1962. H. lacerata was taken on March 31, 1962, near Sterling City, Texas, after an extremely cool winter. These lizards must have been out on warm winter days, for one of the females was gravid when captured. On a field trip to the Big Bend region of Texas in late March, 1962, some specimens of Cophosaurus were taken, but these lizards were not out in abundance. The natives of the region related that they had seen no lizards during the winter until that time.

The lizard species studied are diurnal, coming to the surface of the soil after light and temperature have risen above the threshold for emergence and retiring when either light or temperature becomes lower than that in which the lizard can operate efficiently. The role of the pineal eye in the regulation of emergence time and length of activity in Sceloporus occidentalis was studied by Stebbins and Eakin

(1958). Its role in such regulation for other lizards has not been studied, but it is assumed to be similar.

Although the lizard species in my study are diurnal, several observers have reported on nocturnal activity. Klauber (1939) noted Callisaurus on highways at the following times of night: 7:10, 7:59, 9:45, 11:40 P. M. and at 1:15 A. M. Jameson and Flury (1949) found one H. maculata active at 10:00 P. M., and Woodin (1953) reported two of the same species active about 9:30 P. M., one during a slight drizzle. Milstead (1959) noted that Cophosaurus was easily routed from its nocturnal retreat by close approach. Most unusual is Strecker's (1915) report, in which he quoted the following note on H. propinqua sent to him by a Mr. Mitchell, "These lizards come down to the Gulf beach from the sand-hills and forage among the drift and sea-weed. They make this trip after sun-down and return to the sandhills at daylight." None of my observations showed any nocturnal activity by any of the lizards studied.

My observations of lizards in the enclosure were made from early in the day, before the first lizard emerged, until evening, when the last lizard had retired. Observational data concerned with light conditions, weather, temperature of substrate, air, and lizard, and time of day were taken on 64 days. No lizard emerged before 7:30 A. M. or before the temperature had risen to 22.4°C. In the evening, no lizard was in the open after 7:43 P. M. or when the temperature lowered beyond 30.0°C. On cloudy or rainy days the lizards emerged later or not at all, regardless of the temperature. On occasion, however, if the lizards were out when the sky became overcast and the temperature did not drop appreciably, some lizards remained in the open, even during rain.

Each of the species that I observed exhibited a diel routine which differs from that of the others only in a few details. Each form burrowed into the soil for nightly retreat, rather than seeking shelter under rocks or other surface cover. Minton (1958) stated that H. maculata retires for the night in rodent burrows, but my observations indicate that this would be unusual.

When the lizard was in its nightly shelter, it was only shallowly buried. As the time for emergence neared, the head was raised to the surface, exposing the upper surface. "There the head is in sunlight and blood coursing through a large sinus absorbs enough heat to 'preheat' the body, so that when the lizard emerges, it is ready to take off at top speed." (Bogert, 1959). On partly cloudy days, emergence was later than on clear days.

The time of emergence was variable and depended upon a complex of environmental conditions, but there is a correlation between appearance of the lizard and sunlight shining on or near the retreat. Few lizards emerged before the sun appeared above the rim of the enclosure, which, in July, was about 7:15 A. M. Soon, lizards began to emerge from the sand and to bask. There was a noticeable difference in the time of emergence of the various species. Cophosaurus, H. propinqua, and H. maculata were the first lizards to emerge. Callisaurus and H. lacerata usually emerged later. In an extreme case, on one bright day these two latter species emerged between 60 and 90 minutes after the earliest of the other species. Milstead (1959) reported that his earliest Cophosaurus capture in the day was 8:45 A. M. when the sun arose above

the hills at 7:00 A. M. Present data indicate that emergence of Cophosaurus is earlier than this.

After emergence in the morning, the lizard moves into the sun. It orients and postures in such a way as to obtain maximum utility from the radiant energy. Basking may be on the surface of the soil or upon an inclined or raised surface. Whereas in nature each lizard may bask alone, in the enclosure gregarious basking was the rule, rather than the exception. There appeared to be little segregation according to sex, size, or taxonomic level. This is different from the behavior of the Sceloporus torquatus group of lizards. Hunsaker (1960) found that those lizards aggregate in species groups when basking in mixed populations.

No fine line of demarcation can be drawn between termination of the period of basking and the beginning of the period of "normal" activities. Cowles and Bogert (1944) noted that defecation is closely associated with the attainment of normal operating temperatures. The normal activity range may be thought of as the time when ecological conditions are optimum. During this time the lizard moves about in its ordinary routine: feeding, drinking, mating, asserting, and fighting. In the species studied this time was generally from 9:00 to 11:00 A. M. In later afternoon another period of activity occurred as the ambient temperatures decreased. This period was from 4:00 to 5:30 P. M. during summer months.

Cowles and Bogert (1944) define the "maximum voluntary tolerance" as "The temperature at which the animal retires to shade or to underground retreats. It is heralded by an increasingly noticeable photophobic reaction on the part of diurnal species." A period in the daily cycle of

the lizard was dependent upon this maximum voluntary tolerance. This period extended from the cessation of normal activity around 11:00 A. M. to the resumption of ordinary activity about 4:00 P. M. During this period the lizard ordinarily was quiet in a sheltered shaded place. There was little movement from one spot to another, although an occasional individual might quickly change places. Dominant males and gravid females were the most active during this period. Occasionally lizards burrowed beneath the sand during this period, but most often they stayed on the surface in any kind of shade.

The afternoon period of activity was the reverse of the morning period. As the temperatures lowered in late afternoon, the lizards came forth and moved about in ordinary routine. Soon, however, they began to bask more and more in the sun as it lowered. Gregarious basking occurred less in the afternoon than in the morning, the lizards seeming more intolerant of others.

Some lizards began to retire to their subterranean retreats before the sun set and all were interred shortly thereafter. H. lacerata and Callisaurus were the earliest to retire; the other species later. In July, the earliest burrowing was about 5:30 P. M. and the latest 7:45 P. M. The disposition to burrow appeared variable. An individual might be among the first or the last to burrow on any given day. The only generalization that can be made is that the last to retire almost always was the dominant male of the species.

The manner of retiring was the same for each species. Axtell (1954) referred to it as "shimmy-burial," which is an apt description. The lizard backs up a step or two, lowers the head, and places the snout

in the sand. The front legs are folded back along the body and the snout is placed on the substrate. The head is shaken rapidly from side to side, the movement involving the anterior portion of the body, and the hind legs push forward. The result is a rapid burial as the lizard moves forward. The tail remains above the soil until it disappears with a quick shake.

# CHAPTER VI

## DISCUSSION AND CONCLUSIONS

This study was not undertaken primarily as a taxonomic investigation, but rather as a comparative study of behavioral characteristics, which, of course, have taxonomic implications. Nevertheless, it was also an attempt to ascertain if behavioral traits would assist in determining the correct taxonomic allocation of the lizard currently known as Holbrookia texana (Troschel), the generic appelation of which has been questioned.

The need for other comparative information in addition to morphological and anatomical evidence in determining relationships between groups of animals has been pointed out. Hennig (1950) stated that the object of classification should be the "holomorph," which is all of the characteristics of the individual throughout its life. This view of classification was reiterated by Simpson (1961): "It is a corollary of the fact that organisms are to be classified, not their characters, that the whole organism should be considered in all its parts and all its aspects."

Comparative behavior studies can lead to a better understanding of the relationships among animal species. Hinde and Tinbergen (1958) and Delacour and Mayr (1945) pointed out the value of comparative studies of species-specific behavior. Although species-specific behavior patterns

are most likely to express themselves in courtship or aggressive displays, other criteria, such as temperature preference, have been shown to be specific (Bogert, 1949).

In this study, I found that some patterns of behavior were common among the species studied, and were consistent with patterns which have been described for other genera of the family Iguanidae. These patterns are found in most of the members of the family and are considered characteristic iguanid behavior. Diurnality, territoriality, display, and high temperature preference are considered to be traits shared with other iguanid species. These characteristics are specifically different in detail, however.

Details of morphology and behavior described in preceding sections of this study will be compared and discussed in order to evaluate the taxonomic status and evolution of the lizard species studied.

## Comparison of Species

The widely ranging Holbrookia has inhabited regions in which Callisaurus and Cophosaurus do not occur. The grasslands and aeolian sands do not support populations of either Cophosaurus or Callisaurus, but H. maculata has adapted to open grasslands and H. m. ruthveni and H. propinqua have populated sandy areas. There is overlap in the distribution of H. maculata, H. lacerata, and Cophosaurus, but in these areas they are usually ecologically separated. Cophosaurus is generally associated with rocky areas, whereas Holbrookia are found in flat open areas. Callisaurus lives on desert flats and, where it and Cophosaurus are sympatric, habitat preference separates the two. Thus, there are differences in habitat selection which appears to be characteristic for

each genus. The predilection of Cophosaurus for rocky areas is in contrast to the flat land preference of Callisaurus and Holbrookia.

Holbrookia species are short, stout-bodied lizards with short legs and with tails about as long as the head-body length. These lizards characteristically move only a few feet in a quick dash when disturbed, often continuing these short dashes upon subsequent provocations. In comparison, are Callisaurus and Cophosaurus, whose legs and tails are longer in proportion to the body. These lizards characteristically make long runs when disturbed, sometimes over 100 feet. The pattern of escape is alike in these two lizards. They run for a long distance, usually in an arc, placing a bush or other object between the lizard and the pursuer (Burt and Burt, 1929; Klauber, 1939).

The body shape of Callisaurus is more slender than Cophosaurus, the bodily proportions of Cophosaurus approach those of Holbrookia. Adult size in Callisaurus and Cophosaurus is approximately the same, both being considerably longer than Holbrookia.

In body length Callisaurus and Cophosaurus are alike, but Cophosaurus is more like Holbrookia proportionately. In leg length and escape behavior, Callisaurus and Cophosaurus are alike, but differ from Holbrookia.

Scutellation is basically alike in all of the genera. This has been described by Smith (1946).

The presence of an external tympanum has served to separate Callisaurus from the genus Holbrookia. Holbrookia, on the basis of a lack of external tympanum, included H. maculata, H. propinqua, H. lacerata, (Cophosaurus). Axtell (1958) suggested that "earlessness" arose twice in

the sand lizard group, once for Holbrookia, and later in a form of Callisaurus, here considered as the genus Cophosaurus.

Earle (1961a, b; 1962) made an anatomical study of the middle ear and associated musculature in the sand lizards. As a result of these studies, he stated (1961b), " . . . on the basis of ear morphology alone Holbrookia texana appears to possess characteristics of both Callisaurus and the other Holbrookia. The comparatively unrestricted lateral tympanic pouch and the broadened insertion plate and concave footplate of the extracolumella of H. texana resemble the conditions found in Callisaurus. The extent of lateral notching of the quadrate, the articular cartilage therein, the partial restriction of the tympanic membrane by the depressor mandibulae and its covering by scales indicates a closer resemblance to the genus Holbrookia."

The species of Holbrookia are similar in lack of external tympanum to Cophosaurus, and both of these genera differ from Callisaurus in this respect. The middle ear and musculature indicates an intermediate condition in Cophosaurus, between Callisaurus and Holbrookia.

A basic dorsal pattern of paired blotches is evident in all species studied. In some of the H. maculata subspecies and in H. propinqua, this pattern may be obscured by numerous light spots. A pair of short vertical black bars are located about midway between the legs on the lateral portion of Holbrookia. These bars may be three in number, but are never elongate, reaching to the dorsum. There is only a hint of blue color surrounding these spots in the males. Contrasting with these lateral bars are the elongate paired black crescents which reach the dorsum in Cophosaurus and Callisaurus. In both of these forms the ventral

parts of the bars are expanded. Large areas of blue or green surround the enlarged ventral areas of the lateral bars. The placement of the lateral bars is different in the genera, being placed much farther anteriorly in Callisaurus.

The dewlap is larger in Callisaurus and Cophosaurus than in Holbrookia and is pigmented with a suffusion of ochre. Such color is not present on the tiny dewlap of Holbrookia. The dewlap is expanded in display in all of the forms, the pigmented large dewlap having signal value.

The distinction between color and pattern of Holbrookia and the other two genera is quite marked. The similarity in color and pattern between Callisaurus and Cophosaurus is striking.

Gravid females exhibit a color change in pattern which involves the aquisition of red pigmented spots. In both Callisaurus and Cophosaurus these spots are identical, occurring as enlarged blotches on the sides of the ventral surface posterior to the axilla. In the Holbrookia species, the red spot continues along the edge of the venter and appears on the posterior surface of the thigh. In H. propinqua it appears on the ventral surface of the tail. In addition, there is a suffusion of color throughout the dorsal pattern. H. lacerata females do not acquire red pigment but the dorsum is suffused with yellow or green. The distinction between gravid color in Holbrookia species and females of Cophosaurus and Callisaurus is quite distinct.

Color patterns of black and white alternations appear on the ventral surface of the tail of Cophosaurus and Callisaurus. Holbrookia species do not exhibit such an arrangement, although several small black spots are present on the undersurface of the tail of H. lacerata.

Utilization of the tail in display has been described. Curling and waving are characteristic of the tails of Cophosaurus and Callisaurus. The shorter tails, devoid of subcaudal marks, of H. maculata and H. propinqua are not utilized in this manner. Tail raising appears to be used more in H. lacerata, although only upon provocation. In Cophosaurus and Callisaurus, the tail is curled and waved as part of the ordinary routine.

Both Carpenter (1961a, b; 1962a, b) and Hunsaker (1960) have demonstrated that the push-up of iguanids is species-specific. Perhaps no other behavioral trait distinguishes the genera in the present study as well as the pattern of the push-up. As shown in Fig. 10, the pattern for the species of Holbrookia is the same, varying only slightly in cadence. The patterns for Cophosaurus and Callisaurus are alike in consisting of a preliminary portion and a regular portion, thus differing considerably from the simple pattern of Holbrookia. Callisaurus and Cophosaurus differ from each other in pattern, sequence, and cadence. In push-up behavior, therefore, three distinct patterns are evident, each genus being uniquely different.

Individuals of Callisaurus and Cophosaurus live apart one from another in nature. The territorial proclivity of these lizards is expressed by the formation of dominance hierarchies or autocracies when conditions force several males into the same area. Males, other than the dominant, are completely subordinated and do not utilize basking sites of the dominant or move about in his vicinity.

Holbrookia, on the other hand, lives in closely associated groups in nature. Dominance may be vested in one individual for each

group but other males in his group move about freely. Aggressive interactions are mostly between members of neighboring groups rather than among members of a given group.

Habitat may play a role in this territorial behavior. The small Holbrookia, living in regions of more vegetative cover, may be able to maintain contact between individuals by reduction of the territorial habit. The larger Callisaurus and Cophosaurus live in more exposed situations and tail curling behavior probably aids individuals in finding one another.

Cowles and Bogert (1944) showed that lizards have a narrow range of body temperatures which is quite constant when the lizards are active. The investigation by Bogert (1949) indicated that temperature preference is specific and is characteristic for a natural group, such as a genus, regardless of the ecological diversity of the species. Lizard genera in which all of the species are woodland forms have a preferred body temperature range lower than those genera in which all members are open desert forms. The close kinship of the lizard genera studied is shown by the similarity of the preferred body temperature for each species. Holbrookia, as a genus, is more widespread than either of the other genera. The lower PBT of Holbrookia is indicative of its wider geographic dispersion. Differences in PBT were found in Callisaurus, Cophosaurus, and Holbrookia, which reflect slight phylogenetic divergence.

The species studied are like other iguanids in exhibiting diurnality. An early morning peak of activity ends before noon and resumes on a smaller scale late in the afternoon. This pattern of activity is typical of most diurnal vertebrates during hot weather.

There was little difference noted between species in respect to diel periodicity. There appeared to be a correlation between preferred body temperature and time of emergence in the morning. Callisaurus, which exhibited the highest PBT was the latest to appear each day and was usually the first to retire in the evening.

## Taxonomic Position of Cophosaurus

The close relationship between the sand lizard genera has been pointed out by many authors. The differences exhibited are those which evolved through selection as each genus became adapted to a different ecological niche.

It has been suggested that the lizard known as Holbrookia texana (Troschel) should be considered generically distinct from the other species of Holbrookia (Earle, 1961b). Axtell (1958), in his taxonomic study of the genus Holbrookia, referred to it as Callisaurus texanus. Earle did not commit himself to a definite decision on the matter, but withheld judgment until further evidence became available.

Evidence from the present behavioral study has been given above in comparing the species studied. Pertinent morphological and behavioral information of a comparative nature is summarized in Table 13. The distinctness of Cophosaurus is evident. It is intermediate in many features between Callisaurus and Holbrookia, with the data indicating a closer affinity to Callisaurus than to Holbrookia. The uniqueness of Cophosaurus is most clearly shown in the distinctness of the push-up pattern.

TABLE 13

SUMMARY OF PERTINENT COMPARATIVE MORPHOLOGICAL AND BEHAVIORAL INFORMATION ON LIZARD GENERA STUDIED

| | *Callisaurus* | *Cophosaurus* | *Holbrookia* |
|---|---|---|---|
| Size | Large | Large | Small |
| Legs | Long | Long | Short |
| Body Color | Blue-grey | Blue-grey | Greenish-brown |
| Lateral Pattern | Long bars | Long bars | Short bars |
| Ventral Color Pattern | Large area | Large area | Tiny area or none |
| Dewlap | Prominent | Prominent | Inconspicuous |
| Dewlap Color | Present | Present | Absent |
| Gravid Color | Anterior ventro-lateral blotch | Anterior ventro-lateral blotch | Dorsal suffusion of red or yellow, anterior blotch and posterior of thigh colored |
| Escape Behavior | Run long distance | Run long distance | Run short distance |
| Aggressive Interactions | *Callisaurus* X *Cophosaurus* | *Callisaurus* X *Cophosaurus* | With neither *Callisaurus* nor *Cophosaurus* |
| Curl and Wave of Tail | Yes | Yes | No |

TABLE 13 (Continued)

| | Callisaurus | Cophosaurus | Holbrookia |
|---|---|---|---|
| Tail Pattern | Large black bands | Large black bands | Small dots or no marks |
| Territoriality | Individual | Individual | Group |
| Total Push-up | Two portions | Two portions | One portion |
| Placement of Lateral Bar | Anterior | Posterior | Center |
| Body Shape | Slender | Intermediate | Stout |
| Middle Ear | Distinct | Intermediate | Distinct |
| Preferred Body Temperature | 39.2°C | 38.3°C | 35.7 - 38.1°C |
| Push-up Pattern | Distinct | Distinct | Distinct |
| Tympanum | Exposed | Covered | Covered |

On the basis of the above information, the separation of the lizard species, Holbrookia texana (Troschel), from the genus Holbrookia is warranted. Since it is distinct also from the genus Callisaurus, the name originally applied by Troschel (1852) should be reinstated. The species of this lizard should be known now as Cophosaurus texanus Troschel.

## SUMMARY

Social and display behavior of each species of the iguanid lizard genera Holbrookia and Callisaurus occurring in the United States were studied, both in the field and in enclosures where groups of captive individuals were kept.

It was determined from comparative behavioral evidence in this study, and from published reports upon morphological investigations by other workers, that the lizard currently known as Holbrookia texana is generically distinct, and should be known as Cophosaurus texanus Troschel.

Habitat preference and lookout stations differ among the species. Callisaurus and Holbrookia prefer flat areas, whereas Cophosaurus prefers rocky situations. Holbrookia is more widespread in distribution and more varied in habitat preference than the other genera.

Iguanid lizards exhibit head bobbing or push-up behavior which has been found to be species-specific. The push-ups of the lizards studied were analyzed. Display action pattern graphs were drawn. Push-up patterns for the species of Holbrookia were found to be similar, with minor variations, but unlike the pattern of either Cophosaurus or Callisaurus. Each genus exhibited a distinct pattern.

Assertion push-ups were performed most often by dominant males, but females and juveniles also asserted. Newly hatched individuals exhibited assertion display in the form of push-ups characteristic of the species.

Utilization of the tail in display is described. Those forms which possess black and white subcaudal markings also exhibit maximum utilization of the tail in display. The tail is curled and waved frequently in these forms. It is believed that this display may function as part of the advertisement of the lizard, assisting males and females in finding one another during mating season and also as a territorial declaration.

Courtship and mating are described. The species follow the general iguanid pattern with only specific variations. Homosexual mating attempts were observed, but these were infrequent.

Gravid females were like agonistic males in behavior, whereas non-gravid females and submissive males shared similar traits.

Color change of gravid females is described. This is different in the various species. Rejection posturing of these females is such that the red spotting which appears on gravid females is exhibited to the courting male, and may act as a deterrent to his advances.

Experiments conducted, in which the dimorphic color patterns were switched by painting, indicate that sex recognition is accomplished more by behavioral actions than by color or patterns.

Each species studied exhibited territoriality. Cophosaurus and Callisaurus had numerous interactions with each other, as well as with individuals of their own species, and an autocracy was formed when several males were enclosed together. When the dominant male was removed, another ascended into the dominant position. The species of Holbrookia exhibited a dominance hierarchy, in which the dominant male was somewhat

more tolerant of the other males within his territory than was shown in the other genera.

Cloacal temperatures of lizards were taken in the field at time of capture and at various times in the enclosure. These data indicate that the preferred activity range is from 33° to 41°C. The broadest range is exhibited by H. maculata and is probably a reflection of the broader geographic range of this species. The mean cloacal temperatures of lizards, considered the "preferred body temperatures" were found to be H. maculata, 35.7°; H. propinqua, 37.8°; H. lacerata, 38.1°; Cophosaurus, 38.3°; and Callisaurus, 39.2°C. Body temperatures are controlled by movements into shade and sun, by specific posturing while in the sun, and by selection of substrates and posturing upon these.

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