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GRADUATE COLLEGE

COMPARATIVE BEHAVIOR OF THE HORNED LIZARDS, GENUS *PHRYNOSOMA*, OF THE UNITED STATES

A DISSERTATION

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in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

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Norman, Oklahoma

1963

COMPARATIVE BEHAVIOR OF THE HORNED LIZARDS, GENUS <u>PHRYNOSOMA</u>,

OF THE UNITED STATES

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[illegible]

DISSERTATION COMMITTEE

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Mr. Merrill Cason prepared the drawings of Phrynosoma.

To my wife, Billie, I express my appreciation for her patience, interest, and constant support and encouragement during the course of this study.

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COMPARATIVE BEHAVIOR OF THE HORNED LIZARDS, GENUS *PHRYNOSOMA*, OF THE UNITED STATES

CHAPTER I

INTRODUCTION

History

The study of animal behavior is apparently as old as man himself. A knowledge of the habits of the animals around him has helped man survive in his world as well as aesthetically satisfying his natural curiosity. As the science of zoology has developed, many aspects of the behavior of various animals have been recorded. However, even with this long history, it seems that the study of animal behavior is just now in our own time assuming a prominent place in the halls of scientific endeavor. Man's discoveries about animals and their activities in this century have generated a growing interest in animal behavior and its application. This interest has blossomed into full flower since World War II. Today the study of animal behavior is one of the most dynamic and all encompassing phases of zoological inquiry.

It had long been known that some members of the lizard family Iguanidae bob their heads or even move their entire bodies in a push-up type of motion. During the period 1955 - 1959, Dr. Charles C. Carpenter was engaged in a study comparing the ecology and behavior of *Cnemidophorus sexlineatus* and *Sceloporus undulatus*, two lizards which are common in south-central Oklahoma. During the course of his investigations Carpenter noted that Sceloporus undulatus, which is an iguanid, performed a very consistent type of display involving these bobbing motions (Carpenter, 1962a). The discovery that the display was associated with social behavior, especially territoriality, dominance, and courtship, led to further study of displays among various forms of the Iguanidae. One of the first studies revealed that the display pattern for a species is specific to that species and that it is performed in a definite time sequence (Carpenter and Grubitz, 1961). The material which is presented in this paper is a part of the continuing effort to describe the natural history and particularly the display behavior of the lizards of the family Iguanidae. It is hoped that the information gained in these studies will help to clarify some of the taxonomic problems within the family and contribute to an understanding of the evolutionary development and function of iguanid displays.

There are divergent views as to the phylogeny within the Iguanidae. Camp (1923) expressed the view that Holbrookia, Sceloporus, Phrynosoma, and related genera were primitive forms with the genera Iguana, Dipsosaurus, Cyclura, and relatives as a middle group having as offshoots Basiliscus and Anolis. Mittleman (1942) (Fig.1) and Smith (1946) (Fig. 2) consider the Iguana type lizards as primitive and as giving rise to two branches: one branch (of which Phrynosoma is an offshoot) leads to Sceloporus and the other branch leads toward the Holbrookia and Crotaphytus groups. A third view, proposed by Savage (1958) (Fig. 3), has an iguanine group and a sceloporine group which are distantly related but with no known intermediate forms. In all of these schemes the genus

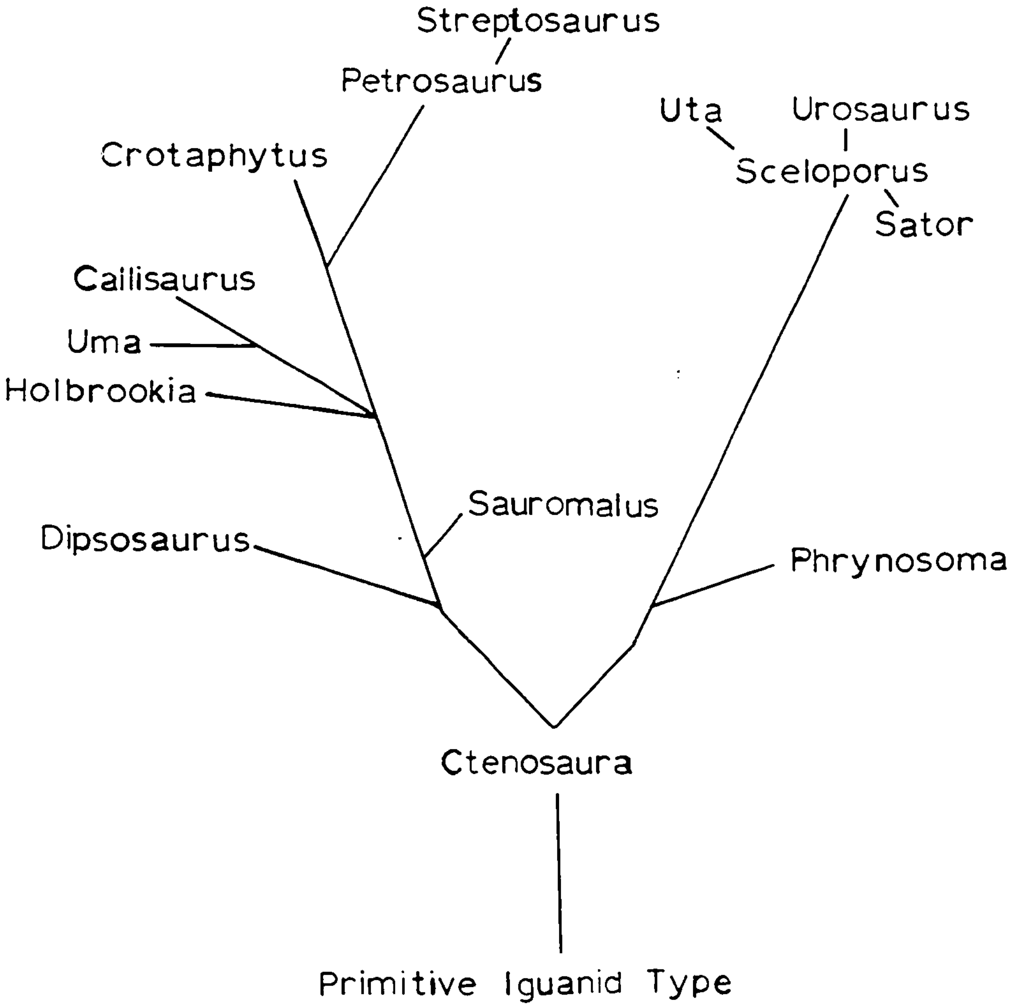

Fig. 1.--Phylogeny of the United States genera of iguanids according to Mittleman (1942).

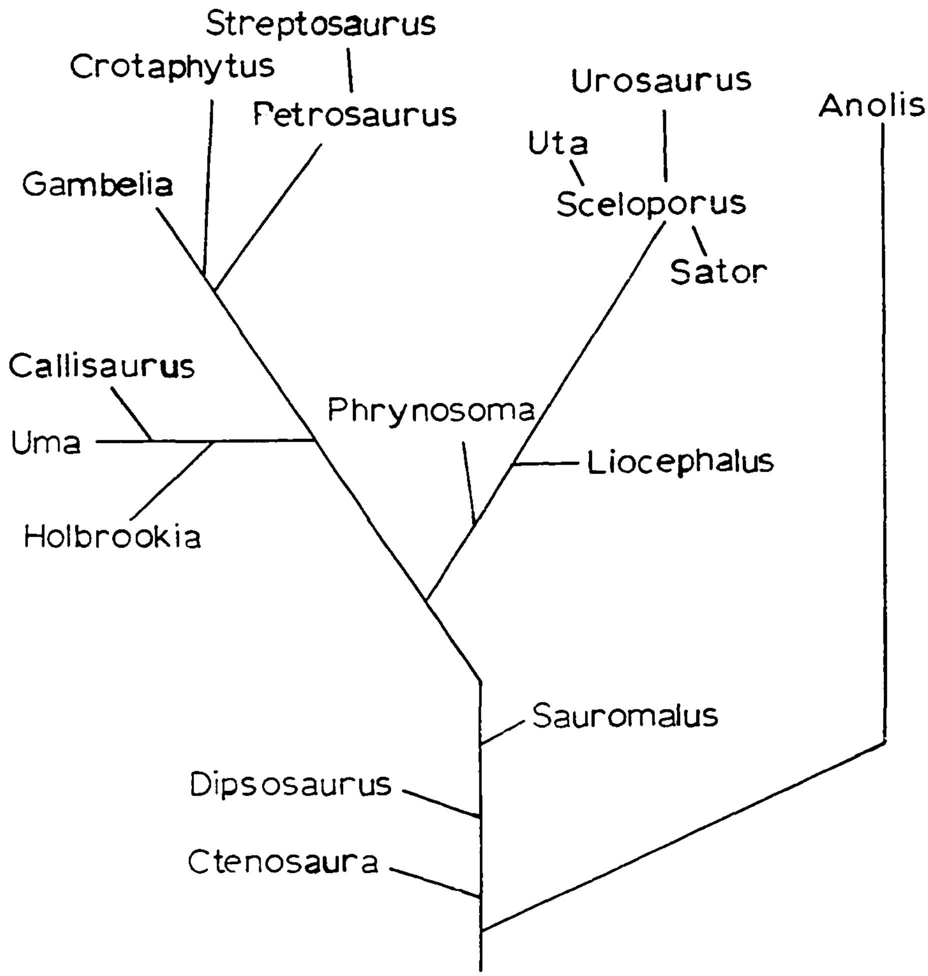

Fig. 2--Possible phylogeny of United States iguanid genera according to Smith (1946).

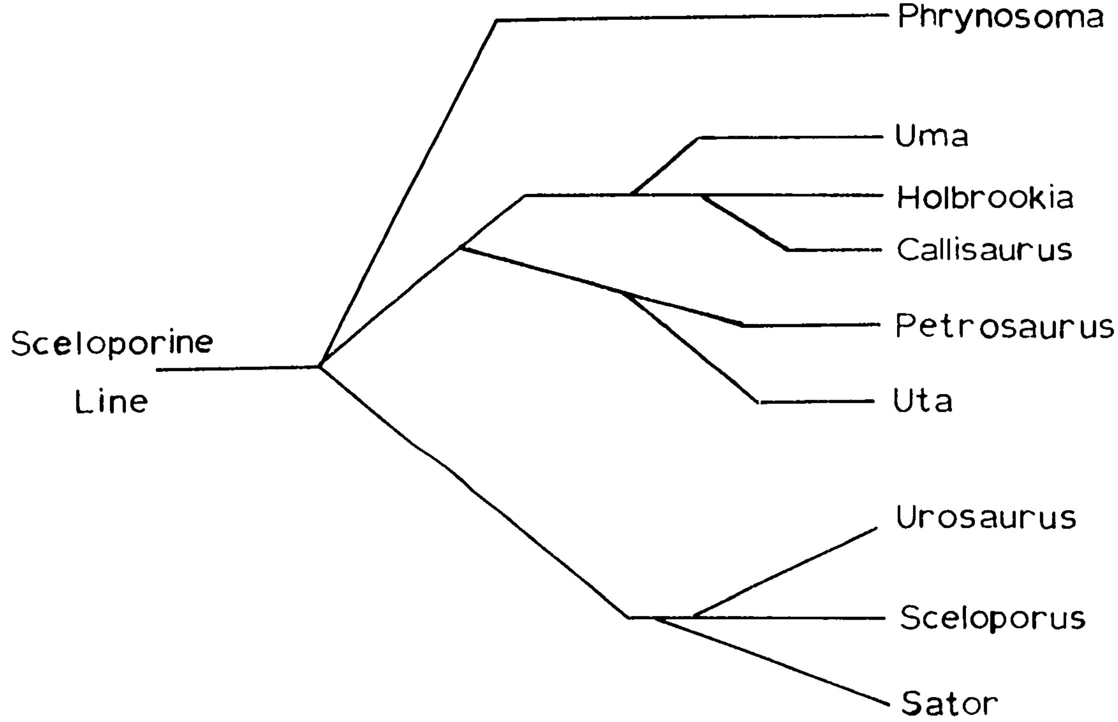

Fig. 3.--Possible phylogeny of the sceloporine line of the family Iguanidae according to Savage (1958).

Phrynosoma is placedsomewhere within a larger sceloporine group. The diagrams presented by Mittleman, Smith, and Savage all clearly indicate that they consider *Phrynosoma* to be a rather early branch from this main line of evolution.

The relationships among the horned lizards have appeared more or less uncertain to a number of workers over the years, but few of them have undertaken a review of the whole group. The most recent and complete review of the genus *Phrynosoma* (Reeve, 1952) recognizes fourteen species with a total of twenty-seven forms. Reeve's postulates as to the relationships of these species are illustrated in Fig. 4.

Paleontology has been of little help in trying to trace the relationships of *Phrynosoma* and at this time there are less than a dozen fossil records. Cope (1873) described a horned lizard from the middle Oligocene of Colorado which he called *Exostinus serratus*. Gilmore (1941) and Smith (1946) have suggested that *Exostinus* is a possible ancestral form of *Phrynosoma*. Fossils of *P. cornutum* are known from the Upper Pliocene of Kansas (Oelrich, 1954) and the late Pleistocene of Arkansas (Gilmore, 1928). Brattstrom (1955) described temporal fragments of *P. orbiculare* and of a *P. josecitensis*, which is known only from this fossil, from the Pleistocene of San Josecito Cavern, Nuevo Leon, Mexico.

With the absence of a fossil record to aid them, taxonomists have been forced to rely entirely upon morphological characteristics in trying to trace the phylogeny of this group. It is hoped that the information presented on the following pages will complement these morphological characteristics and prove useful in helping to clarify the position of not only this but other lizard groups.

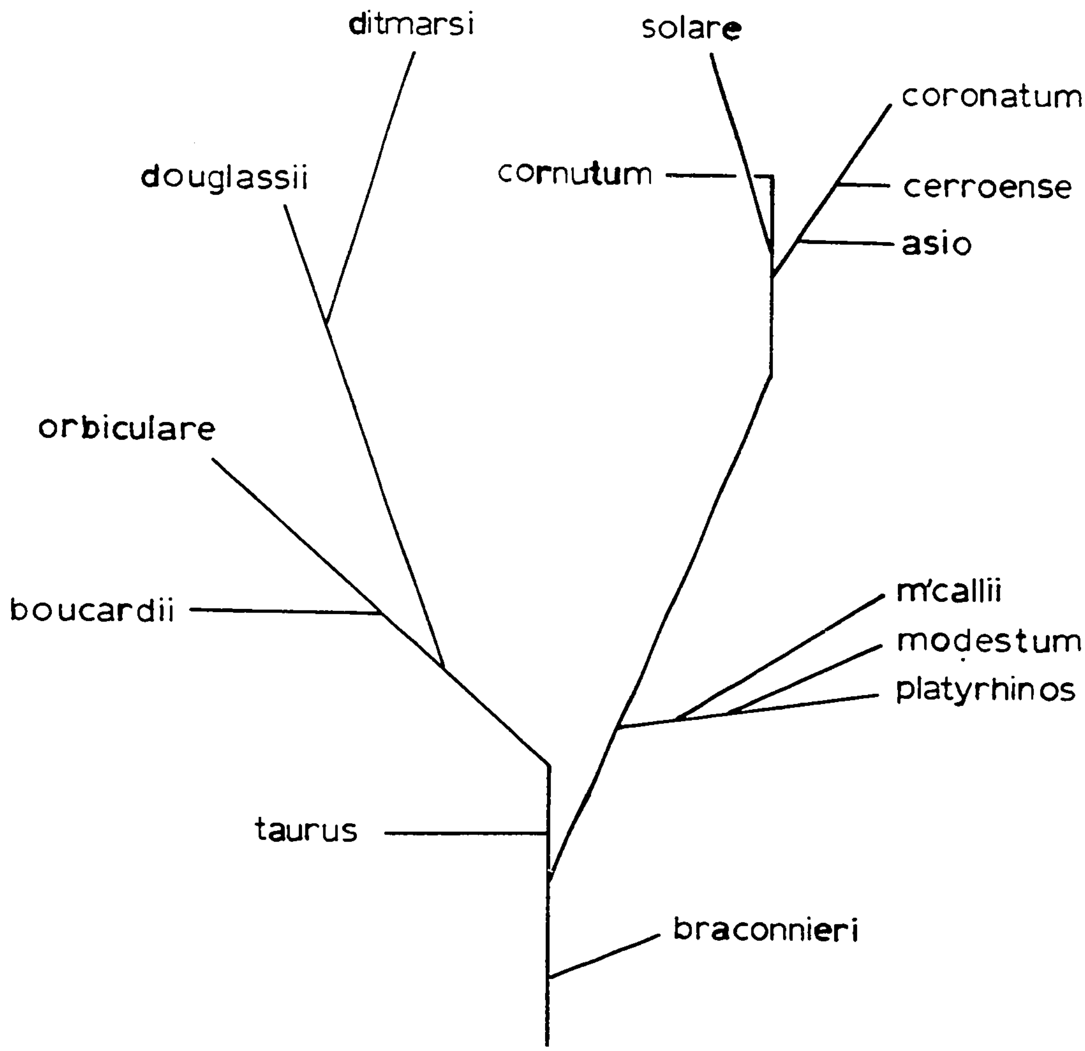

Fig. 4--Possible phylogeny of Phrynosoma according to Reeve (1952).

Distribution

Seven of the species recognized by Reeve are not found in the United States. Most of these apparently have a rather limited distribution in Mexico and Guatemala and are not well represented in museum collections. The other seven species are found in the United States. My research has been restricted to six of these species. A short synopsis of the distribution and general ecology of the United States species is given on the following pages.

Phrynosoma platyrhinos (Fig. 5): The geographic range of this species extends throughout the desert areas of the western United States from eastern Washington on the north to the Gulf of California on the south (Fig. 6). Though it has been taken at an altitude of 6500 feet it is not considered a montane inhabitant. It is associated with broad, flat, areas having scattered cover of sagebrush or creosote bush and other low scrubby desert plants. Some patches of relatively loose soil or sand are scattered through these areas where rock and gravel cover a large portion of the ground. A total of twenty-one individuals have been observed in this study, thirteen being the most on hand at any one time.

Phrynosoma m'calli: The geographical distribution of this lizard is very restricted (Fig. 6). Ecologically it is even more restricted, being found, like the genus Uma, only in areas of fine windblown sand. In the fall of 1960 we thought we had one specimen of this species, but subsequent study has cast doubt on the identification of the specimen. The meager information obtained from this specimen does not differ from other species however. Norris (1949) found that two specimens a day was excellent collecting in the area where he found this species most abundant.

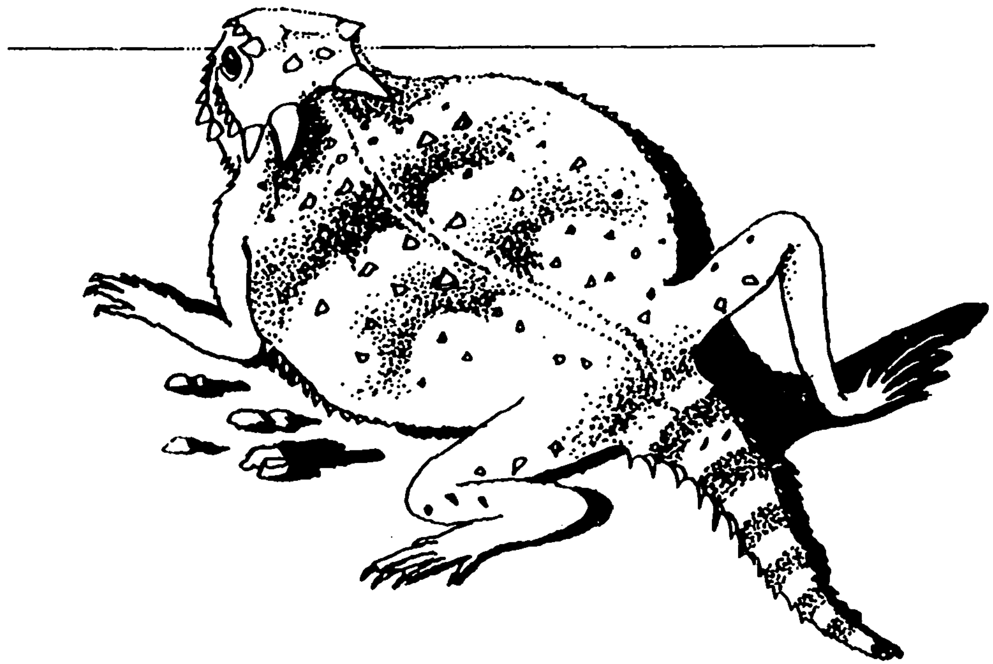

Fig. 5.--Phrynosoma platyrhinos flattened and tilted to intercept the sun's rays at a ninety degree angle.

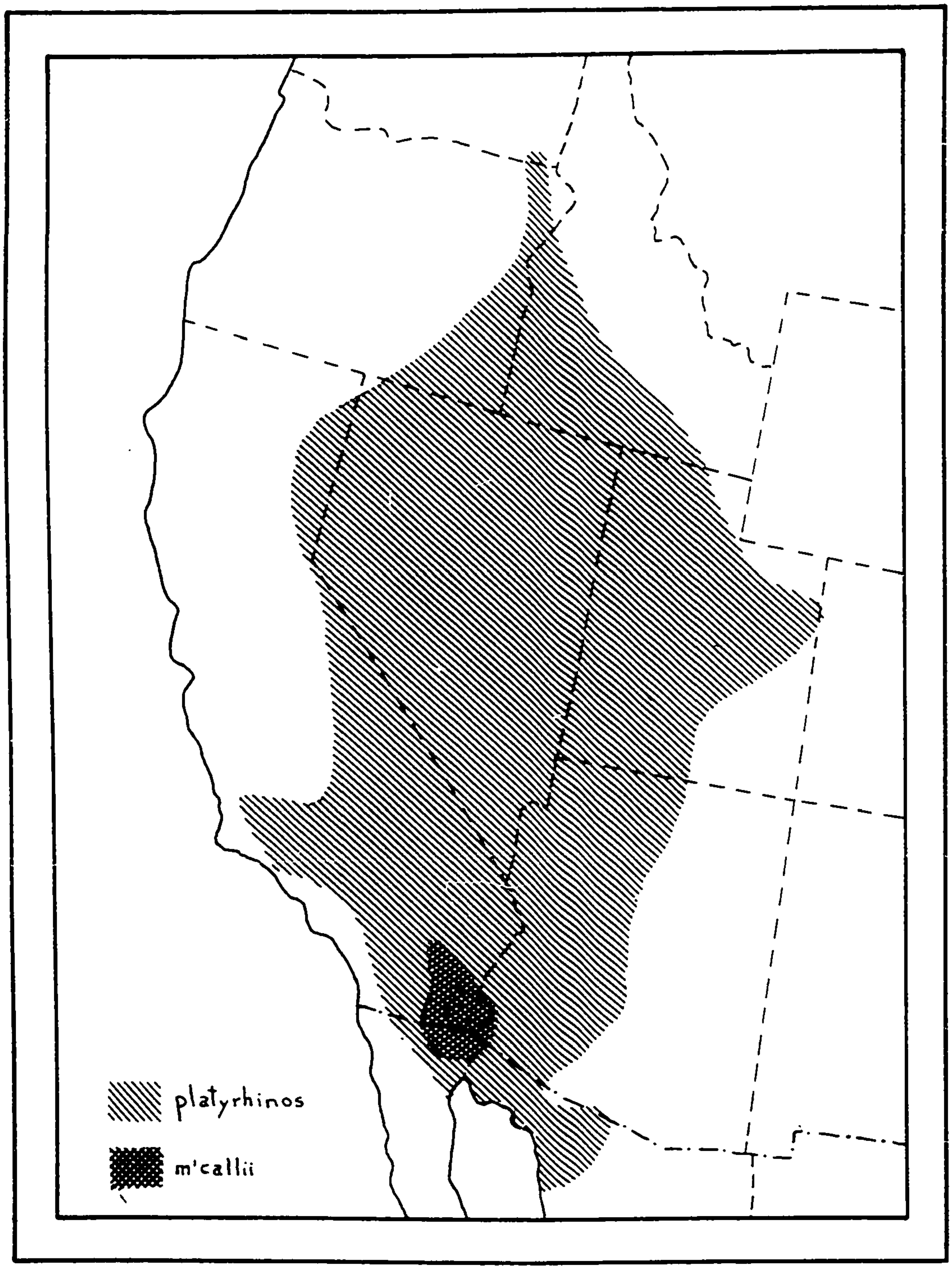

Fig. 6.--Geographic distribution of Phrynosoma platyrhinos and Phrynosoma m'calli.

Phrynosoma modestum (Fig. 7): This lizard is found on the high plains of western Texas, New Mexico, southeastern Arizona, and Mexico (Fig. 8). Throughout this area it has been found in several plant associations and on a substratum varying from blow sand to rocky slopes. Over the course of the study I have observed thirty-two individuals, eleven being the most on hand at any one time.

Phrynosoma coronatum (Fig. 9): This species, the largest horned lizard in the United States, is found in the western half of California from the latitude of Sacramento southward to the tip of Baja California (Fig. 10). Though the herpetological fauna of California has been studied extensively, information concerning the ecology of this species is strangely lacking. It apparently ranges eastward to the passes leading into the desert but does not enter the desert. Like other members of the genus it apparently prefers relatively open areas of grass and scattered bushes. A total of thirteen have been available during the course of this study, seven being the largest group at one time.

Phrynosoma cornutum (Fig. 11): The Texas Horned Lizard is the best known of all the horned lizards. Its probable natural range (Fig. 12) is extensive and more or less permanent populations have been reported as established in various other parts of the nation, especially the southeastern states. It is found in many of the drier ecological associations throughout its range. Generally the vegetation will be sparse or disturbed in some way. Rocky or eroded areas, vacant lots, and flower beds are the places where this species may be found. In fact, this species may be more abundant in the latter two areas than "in the field." One hundred ninety-one individuals have been used in this study, several being available at all times.

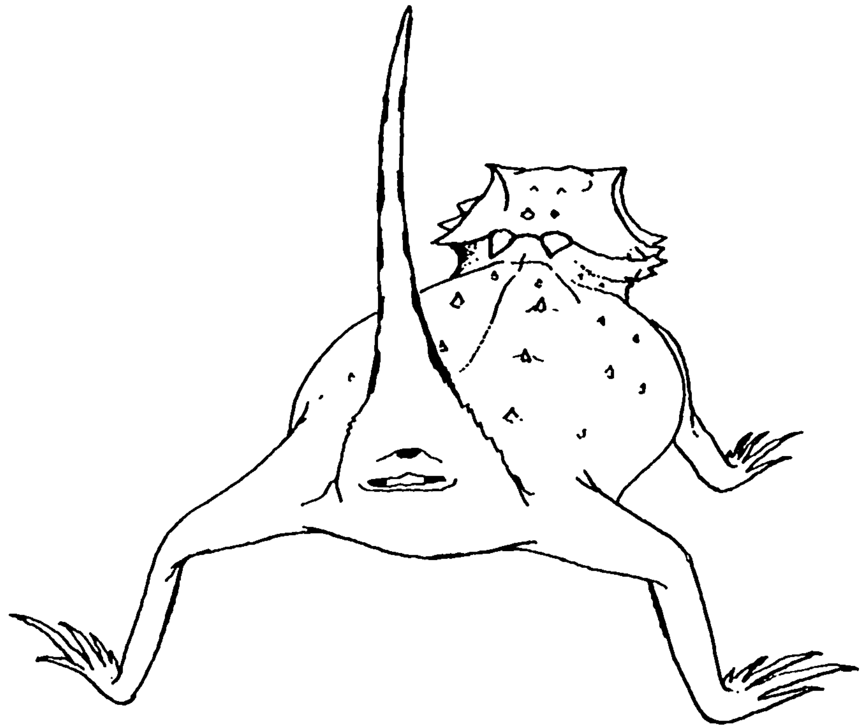

Fig. 7.--Phrynosoma modestum in the rejection posture typical of the genus.

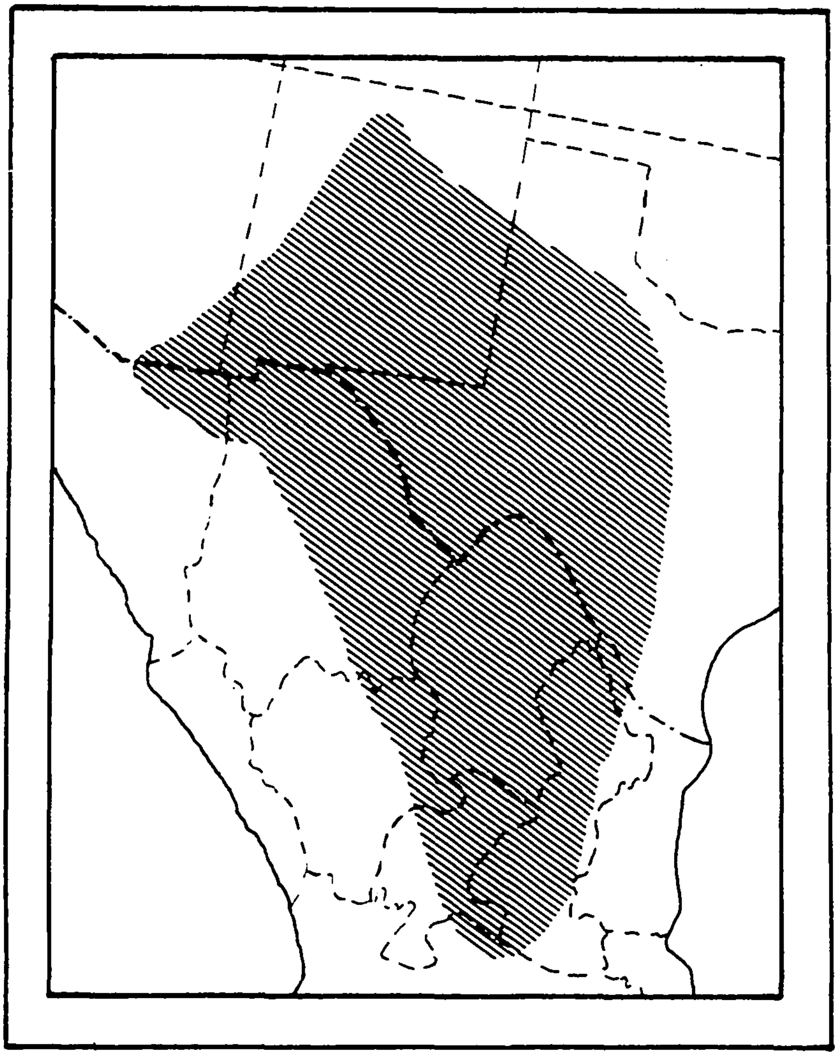

Fig. 8.--Geographic distribution of <u>Phrynosoma modestum</u>.

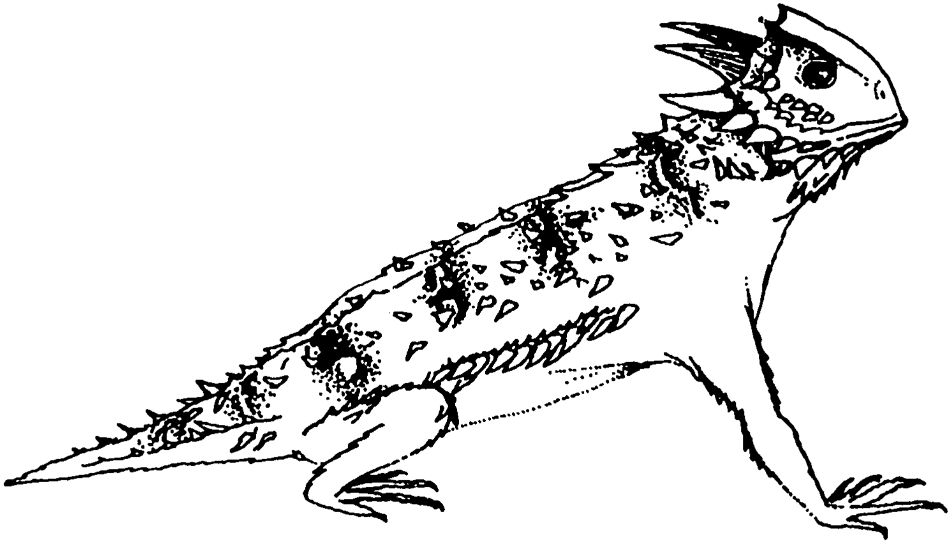

Fig. 9.--Phrynosoma coronatum in alert posture.

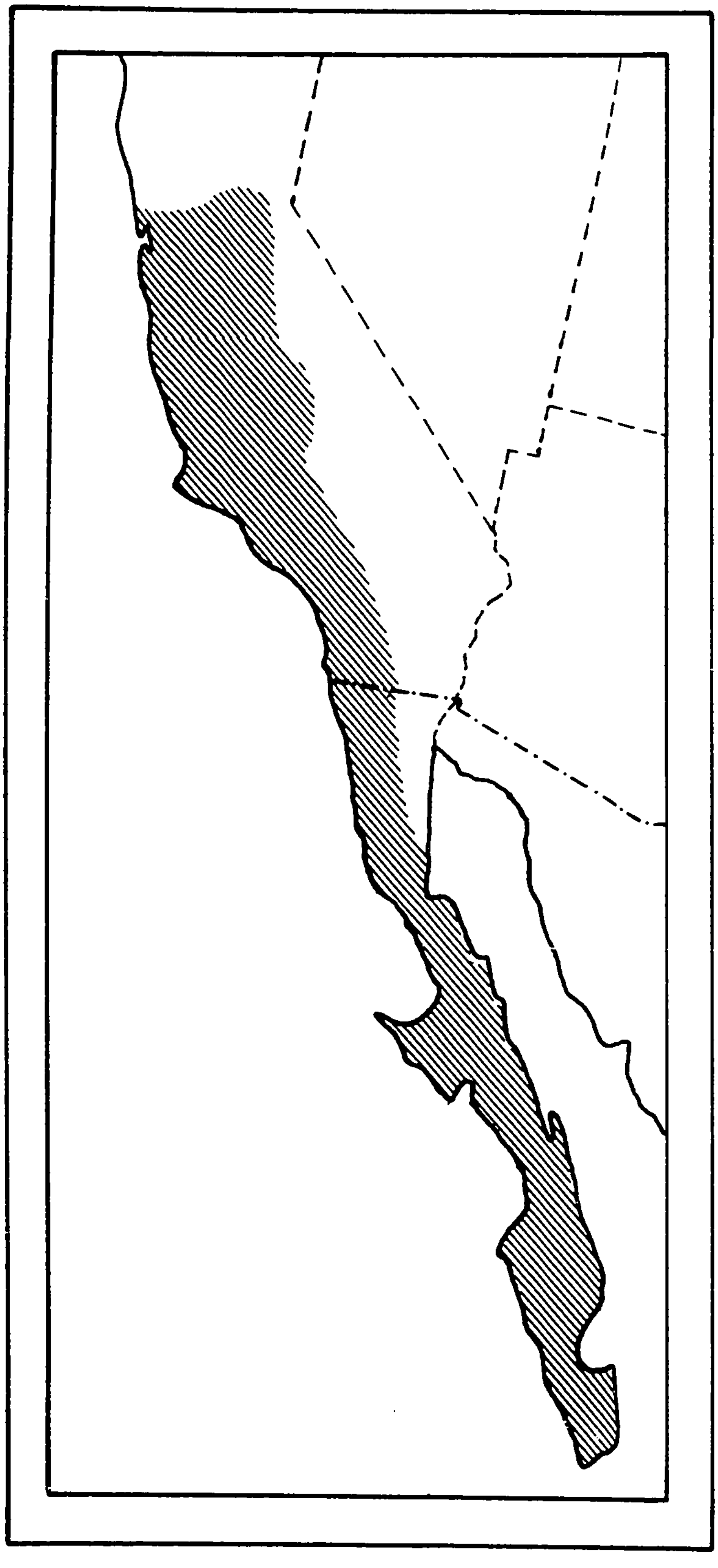

Fig. 10.--Geographic distribution of Phrynosoma coronatum.

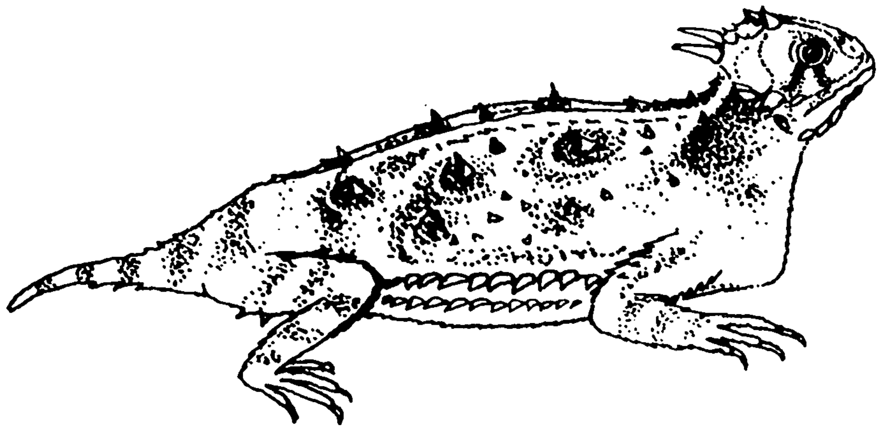

Fig. 11.--Phrynosoma cornutum in rigid defensive posture.

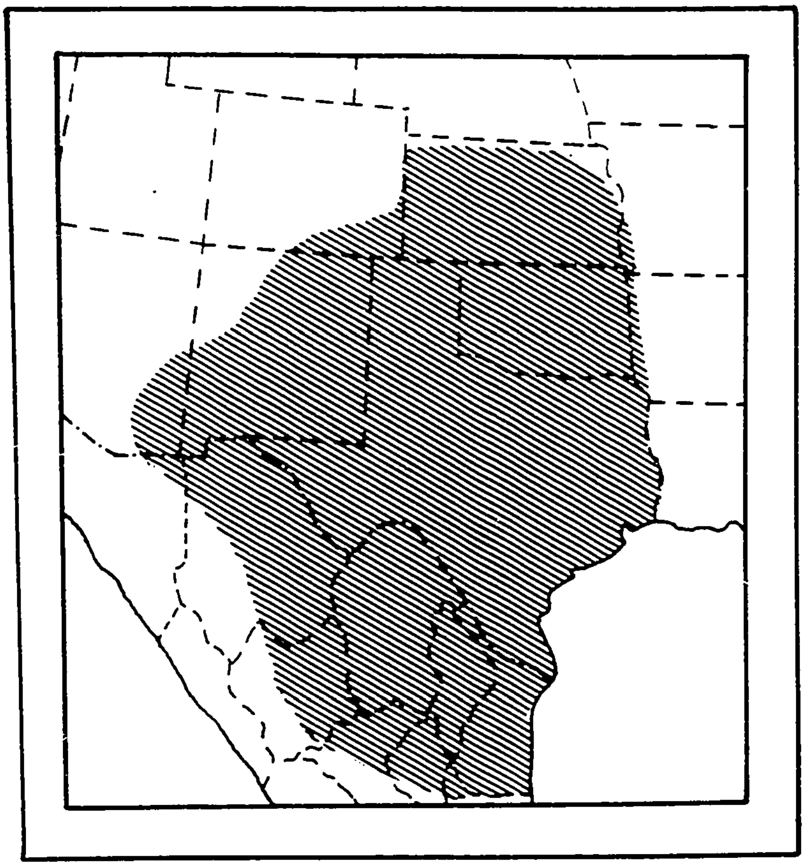

Fig. 12.--Geographic distribution of Phrynosoma cornutum.

Phrynosoma solare (Fig. 13): This species is found in the southern half of Arizona and its range extends southward to just beyond the borders of the Mexican state of Sonora (Fig. 14). Most reports mention that it is found in either a mesquite, greasewood, or cresote bush association. In this study I have observed one individual and have utilized motion pictures made by Dr. Carpenter of three individuals belonging to Dr. Virgil Dowell.

Phrynosoma douglassi (Fig. 15): This is the widest ranging of all the horned lizards (Fig. 16). Like the others it is found in arid situations with loose soil. The area is often rocky with a more or less open type of vegetation. This species has been taken at altitudes ranging up to 9500 feet. At the higher altitudes it is found in the piñon-juniper and ponderosa pine associations. Specimen records show that in Texas, New Mexico, southern Arizona, and Mexico this lizard's distribution follows that of the mountain chains very closely. Conversations and correspondence with persons living in areas where this form and other forms overlap geographically indicate that there is an altitudinal separation between P. douglassi and sympatric forms, P. douglassi being found at higher elevations. I have used ten individuals in this study, four being the most on hand at any one time.

Methods and Materials

The lizards used in this study were obtained by three methods: field trips, gifts, and purchase. Friends, relatives, and herpetologists have been most kind and helpful in sending lizards from areas in which they reside. Without these contributions this study could not have been conducted. In the spring of 1962 an attempt was made to purchase some

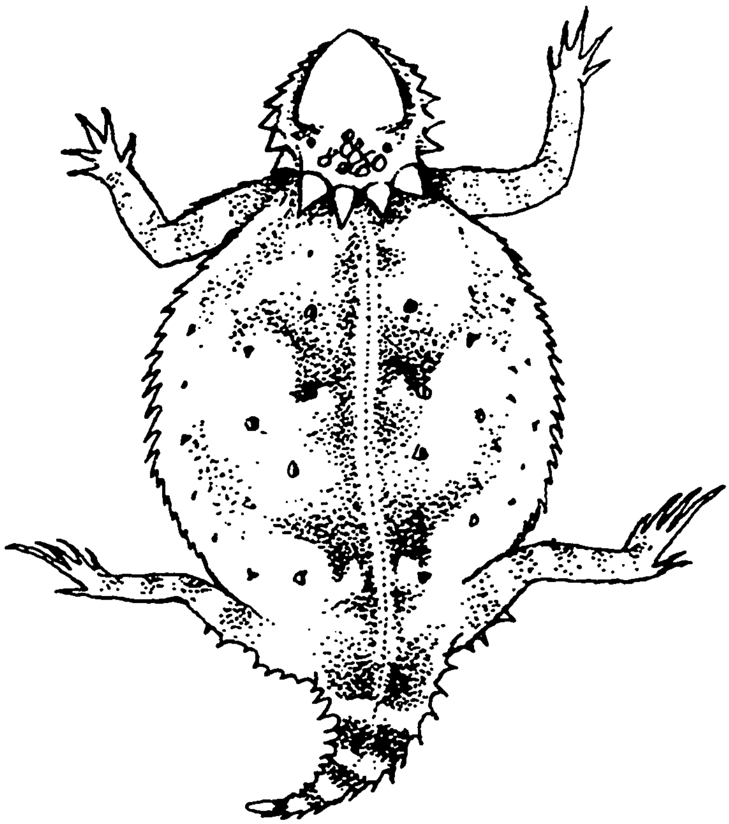

Fig. 13.--Phrynosoma solare flattened against the ground, as seen from above.

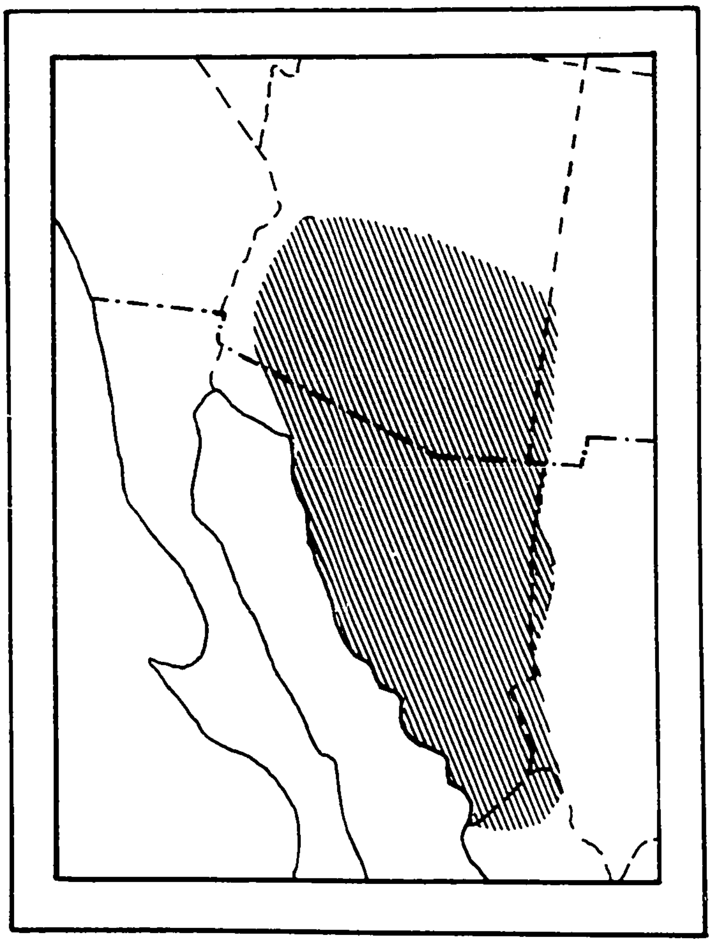

Fig. 14.--Geographic distribution of Phrynosoma solare.

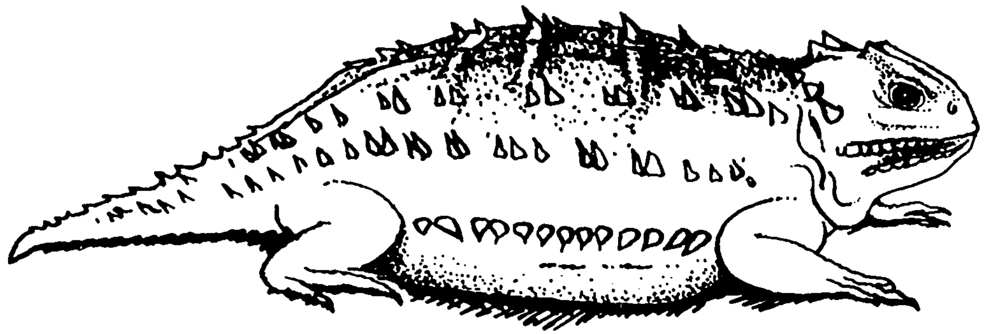

Fig. 15.--*Phrynosoma douglassi* in inflated defensive posture.

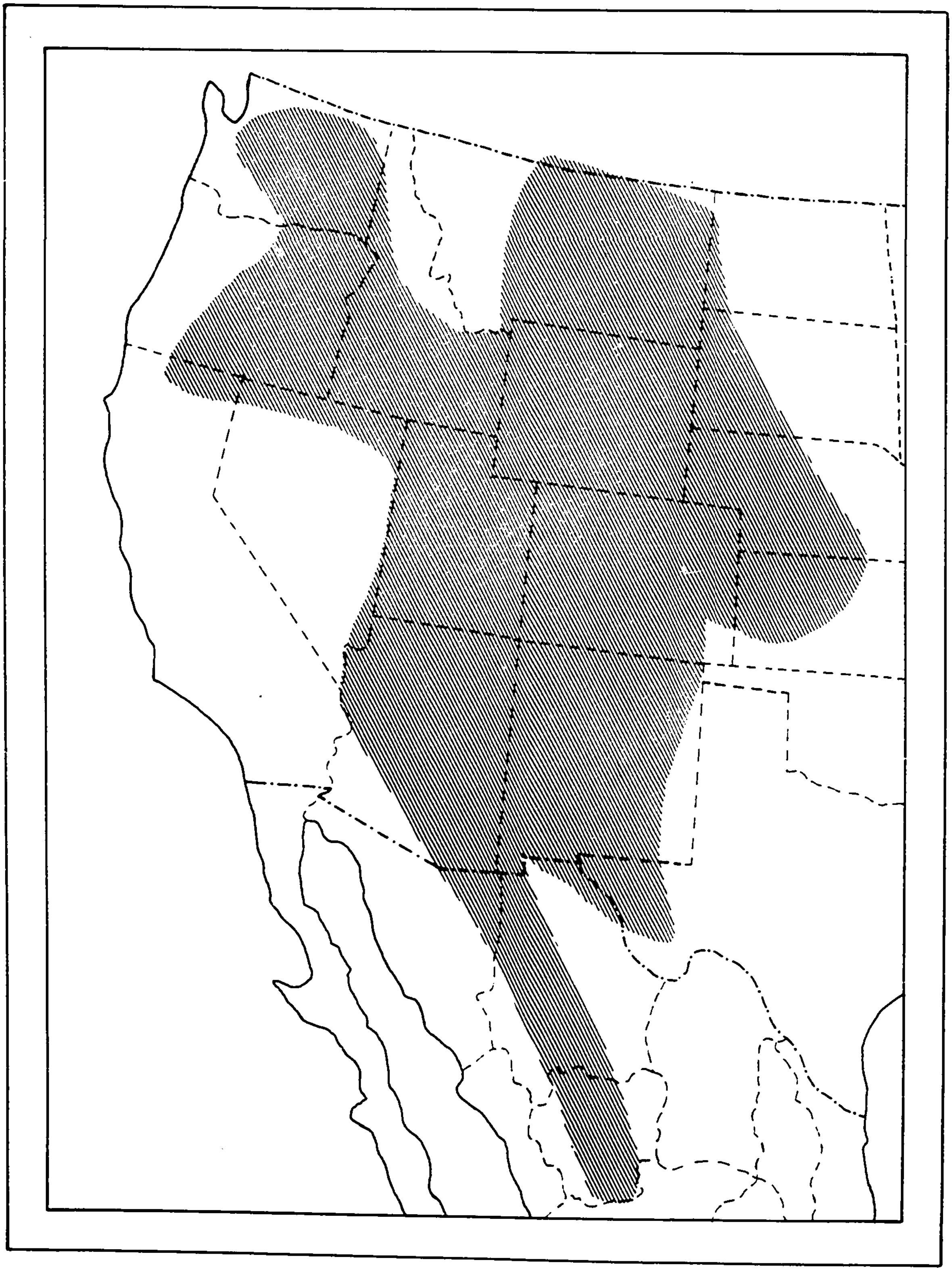

Fig. 16.--Geographic distribution of *Phrynosoma douglassi*.

of the western forms included in the study, but only the more common *P. coronatum* and *P. platyrhinos* could be supplied by dealers.

Five field trips were made to collect lizards. In the spring of 1960 our field party visited southeastern California, southern Arizona, southern New Mexico, and western Texas. In late summer of 1960 I visited portions of western Texas and southeastern New Mexico. In the spring of 1961 our field party visited central and southern New Mexico, central and southern Arizona, and southern California. In the spring of 1962 field work was confined to the Big Bend region of Texas, and in June 1962 a three day trip was taken to the Sterling City area of Texas. Though the horned lizards are well known by local inhabitants and are reported to be "common" and "everywhere," finding them on collecting trips is another matter. These lizards are extremely difficult to locate in the field and only a few were collected on any given field trip.

This study was conducted in part at the University of Oklahoma Biological Station and in part at the Animal Behavior Laboratory on the North Campus of the University of Oklahoma at Norman. At the Biological Station the lizards were confined and studied in an outdoor sheet metal enclosure 15 x 15 x 3 feet and in 40 x 40 x 20 inch cages. The floors of the enclosure and cages were covered with fine sand. Rocks, cement blocks, logs, and grass were placed in the enclosure and cages at various times and in various configurations. The lizards had access to a water dish at all times. The lizards were fed red agricultural ants, various small arthropods obtained by sweep-netting, and the insects attracted to a light suspended over the enclosure at night.

In Norman the lizards were kept in similar enclosures and cages. One of these enclosures was set up inside the building during the winter.

Mealworms served as the primary food during the winter months.

A system of toe clips was used for permanent marking of the lizards. Model airplane dope in various color combinations was used in making marks for ready individual identification in the enclosures.

Methods used in the analysis of specific types of behavior are described in the appropriate sections of the paper.

CHAPTER II

PRELIMINARY OBSERVATIONS

Senses

The stimuli received from the environment are the triggers which set the various behavior patterns of an animal into motion. I have not attempted to study the extent of development, relative importance, or particular part played by any one sense in the behavior of *Phrynosoma*. However, it is appropriate that the observations made concerning the senses be recorded here. My own observations have not detected any difference in the use of the senses by any of the species, thus the statements which follow apply equally to all species.

In many animals, and especially in lizards, vision is an important sense. Several workers have studied the eye of *P. cornutum* in some detail. *Phrynosoma* has a purely cone retina (Crozier and Wolf, 1941; Keeler, 1930). The pit of the fovea has no cones, making the lizard more dependent upon movement to detect objects (Walls, 1942). While *Phrynosoma* may see an immobile object, movement seems to be necessary to elicit a reaction from the lizard. Food items must move before they are snapped up and any movement by another animal in the vicinity attracts their attention. As an example of acuteness and range of vision, I have seen horned lizards stop, look up, and follow the flight of an airplane across the sky several hundred feet above their enclosure at the Biological Station. One of the better methods of catching a lizard without harming it is by means of a noose on the end of a long thin pole. In some of our studies we needed to noose an individual repeatedly. The lizard soon learned the meaning of the pole and noose. When it saw the noose approaching the lizard would take evasive action. This indicates not only good eyesight but also a type of conditioning.

The eyes of Phrynosoma are located laterally on the head. Lizards' eyes are structurally modified to improve binocular vision (Walls, 1942), but Phrynosoma does not appear to have good binocular vision at close range. As one approaches an object which it is watching, such as an ant, the head will turn so that one eye faces the object. Milne and Milne (1950) have described similar behavior.

The extent of development and the function of the chemical sense is unknown. The Jacobson's organ is present and the active Phrynosoma is frequently seen to test the ground, objects of the environment, and other lizards with its tongue. I have not been able to determine the part played by this testing in the behavior of Phrynosoma. The performance of the testing action does not seem to depend upon the lizard's familiarity with the environment, upon the presence of food, or upon the sex of the other lizard. I have not seen a Phrynosoma perform any action subsequent to testing with its tongue that could be attributed to information received by that means. Hunsacker (1960) tested the reaction of several Sceloporus species to femoral pore secretions. The femoral region is frequently the portion of the body tested by one iguanid when it approaches another. By means of preference tests he showed that a *Sceloporus* preferred to remain with a lizard sprayed with an extract of the femoral pore secretions of its species rather than a lizard sprayed with the secretions of a second species.

The function of the ear in the behavior of lizards is unknown. I have observed nothing that would indicate hearing or a response to vibration. Equilibrium is fairly well developed. A *Phrynosoma* which falls on its back will struggle to right itself, throwing the head back and thrusting it against the ground, arching the back, and waving the legs vigorously. A *Phrynosoma* which climbs the wire walls of its cage and falls off after clinging there for a time, will frequently land on its feet.

Food and Eating Behavior

Phrynosoma will apparently eat or attempt to eat any small object which exhibits some degree of independent motion. *P. modestum* has eaten lead shot rolling down an incline and sand grains which blew by it (Weese, 1917a, 1919). Berries of *Lycium andersonii* with stem and calyx attached found in the stomach of *P. platyrhinos* led one investigator (Banta, 1961) to believe that the berries were nipped off. I cannot believe that any of the *Phrynosoma* I have observed are deliberately herbivorous. Any plant material ingested by them is probably purely accidental or a case of mistaken identity.

The large argicultural ants are a favorite food item of all the United States species of *Phrynosoma*. Almost any other insect of appropriate size (adults and active larvae) found in the habitat will be eaten. An extensive literature on food habits has been reviewed by Milne and

Milne (1950).

When prey animals are actively moving about in the vicinity of a horned lizard it stands stolidly in one place, the head and tongue darting out to snap up victims which pass within range. Standing beside an ant trail a horned lizard may consume hundreds of ants in this manner with very little effort. Slowly moving prey animals may be stalked by the horned lizard. It will approach the prey slowly. The head is turned to one side so that one eye has a full view of the prey. The tail is extended and the end twitches slowly. Suddenly the head darts forward and the prey is snapped up. If the prey is large or too long to be engulfed when it is caught, the lizard shakes its head violently and rubs the jaws against the ground, backing up a few steps at the same time. This action kills the prey and protruding parts are broken off. The prey is then easily swallowed. Gulping motions are seen within a few seconds after prey is snapped up. Several investigators have observed similar behavior (Milne and Milne, 1950).

The agricultural ants and the horned lizards have apparently had a long relationship for each has developed a healthy respect for the other. If the horned lizard suddenly finds itself surrounded by a swarm of ants, it will make a violent effort to get to another area. However, if an ant climbs onto the back or head of the lizard, the lizard immediately freezes and remains still until the ant leaves or until it reaches a position on the head where it can be shaken off or snapped up. A horned lizard unable to escape from the ants may be bitten repeatedly until the lizard is finally killed. On the other hand the ants exhibit some "knowledge" of the predatory role of the horned lizard. Dr. Hobart Smith conducted a series of experiments in which the activity of an ant nest was controlled by the presence of several _P. cornutum_ (Milne and Milne, 1950). All attempts to establish an ant colony in my experimental enclosures were apparent failures. In one instance a colony was dug up and placed in one of the indoor enclosures. Only a few horned lizards were in this enclosure, but within two days not an ant was to be seen. Seven months later when the lizards were removed preparatory to moving to the Biological Station, ants reappeared and upon investigation a thriving colony was found. It seems that the ants will not venture out of the nest if a horned lizard is present.

I have observed many instances of apparent social facilitation in the feeding of _Phrynosoma_. Movement toward food and feeding motions by some of the lizards will alert and attract others. Under other conditions, a _Phrynosoma_ pays little attention to the movement of other lizards around it.

Horned lizards usually show an apparent lack of interest in water, a fact that has been commented upon by many authors. _P. douglassi hernandesi_ has been reported to drink (Dodge, 1938) and _P. cornutum_ may sometimes lap water (Winton, 1917). In my enclosure horned lizards were seen licking water from a water dish and, more frequently, licking drops of dew from blades of grass. During light rain or when the enclosure was sprinkled with a hose, the horned lizards would come out into the sprinkle and flatten themselves so that the largest possible expanse of body surface was exposed to the falling water.

Defecation

Most of the waste products of metabolism and undigested material are passed from the body of the horned lizard in the feces. The urine of P. cornutum is primarily uric acid (Weese, 1917b), and that of other horned lizards probably has a similar composition. The typical fecal pellet has a white blob of uric acid at the end which is extruded first, followed by a large mass of undigested insect parts. This type of fecal pellet is typical of all lizards.

The behavior during defecation as seen in the horned lizards is similar to that of other iguanids which I have observed. The body is raised on all four legs, the tail is elevated, and the lizard leans forward. Straining movements are then evident in the pelvic region as the fecal pellet is passed from the cloaca. After the fecal pellet drops free the lizard will move forward a few steps, then lower the cloaca to the ground and drag it over the surface for a few steps before the tail is lowered and the lizard's attention is directed elsewhere.

It has been suggested that defecation might occur at a particular time of day or at a particular time in the activity cycle. It has also been suggested that the feces might be used in signposting. I have not been able to find any evidence to support these suggestions. The horned lizards apparently defecate when and where the urge strikes.

Defense

The horned lizards have developed several means of defense. Some of these are of a passive nature and apparently are of value in helping the lizard escape detection. Other more active defensive activities are brought into play if the lizard is molested by another animal.

When another animal, approximately its own size or larger, is first detected by a horned lizard its first act is to crouch against the ground with the head slightly elevated and the body more or less flattened. If the other animal moves closer to its position, the horned lizard will dash toward a nearby place of protective cover such as into tall grass or under a bush or rock. At the end of the dash the horned lizard will flatten its whole body against the ground and remain there unless the other animal makes a pass directly at it. The protective coloration is very effective and unless one notes the exact spot where the lizard stops it is very difficult to detect. Richardson (1915) and Linsdale (1938) have commented on the propensity of P. platyrhinos to run under the low desert bushes when disturbed. On the other hand P. modestum has been described as relying solely upon its coloration for protection (Burt and Burt, 1929; Milstead, 1953). Norris (1949) describes P. m'calli, a strictly sand dwelling form, as dashing away and then either pressing itself flat against the sand or diving beneath the surface. All of the Phrynosoma which I have been able to observe have acted in the manner which I have described above.

The horned lizards will all wiggle and gyrate the head when they are picked up. These wild movements serve to throw the spines and horns against the predator. Klauber (1939) reported that the spines of P. m'calli are sharp enough to pierce the skin during such a performance. I can attest to the fact that the horns of P. cornutum, P. platyrhinos, P. solare, and P. coronatum are also sharp enough to pierce the skin.

A short time after being picked up a horned lizard ceases its violent struggles. Now the lizard assumes the attitude shown in Fig. 11. This attitude will be maintained as long as the lizard is handled. The body will become puffed up to the extent that it looks like a small spiny ballon. This behavior is especially noticeable in P. douglassi.

While in this stiff, puffed up attitude the lizard will respond to stroking on the back by tilting the body toward the side that is stroked.

Another defensive performance is given by _P. modestum_ and _P. cornutum_. As a second lizard approaches, the first will drop a shoulder toward it. This has been seen several times and was done by at least two different individuals of each species. It is by no means a common movement, there usually being no apparent acknowledgement of the presence of another lizard.

P. cornutum has been described as fighting by puffing and blowing (Winton, 1917) and as defending itself successfully against a house mouse (_Mus musculus_) by facing it with open mouth (Burt, 1927). I have once or twice seen individuals of _P. cornutum_, _P. coronatum_, and _P. platyrhinos_ puff up, hiss, and hop up when a hand approached them. A rather vivid account of a display of this type by a _P. platyrhinos_ is given by Lowe and Woodin (1954).

Perhaps the most famous means of defense used by the horned lizards is the squirting of blood from the eye. I have never been fortunate enough to observe this phenomenon myself, but it is a well documented act. The first published account of this strange occurrence (Wallace, 1871) apparently drew little notice. O. P. Hay was surprised by the blood squirting of a _P. coronatum_ in his possession and induced the lizard to perform several times. He found that this ability to squirt blood was fairly well known to persons who handled "horned toads" but he could find no references in the literature. The note he subsequently published (Hay, 1892) aroused a continuing interest in the phenomenon. Investigations of the mechanism of this blood squirting have revealed that the lizard can inhibit the flow of venous blood from the sinus orbitalis and as the pressure in the sinus mounts the blood is forced through the membranes around the eye (Bruner, 1907; Burleson, 1942).

Coloration

Coloration and the mechanism of controlling color are important factors in two different aspects (protective coloration and temperature control) which contribute to the ability of the horned lizard to survive in its habitat. Each species has a pattern of light-bordered dark spots on the back which act as a camouflage pattern to break up the ground color of the back which is very nearly the shade of the earth where the lizard lives (Durham, 1956; Hoffman, 1879, King, 1932, Klauber, 1939; Lawrence and Wilhoft, 1958; Lowe, 1947; Milstead, 1953; Minton, 1958; Stejneger, 1890; Strecker, 1909; Tanner, 1930). This matching of color between lizard and soil provides a very effective means of permitting the lizard to escape detection by another animal. Adult lizards which have been in captivity through several sheddings do not lose the shade of the ground color evident at capture, even though kept in a habitat with soil of a different color. Though this fact might seem to indicate a genetic factor in the local population which controls the ground color, there is some evidence that this is not entirely true. All the young *P. cornutum* which have been hatched during the course of this study have been dark brown in color though the females which laid the eggs had ground colors of varying shades. The young of a white female *P. modestum* were pink when hatched. One group of thirty young *P. douglassi* varied in color from reddish through yellowish-brown to nearly solid dark grey

(Woodin, 1953). Bundy and Neess (1958) have studied the coloration of P. modestum by means of a photometric technique. Lizards collected from several different areas with different soil colors were tested. Comparison of lizard and soil showed a positive correlation in color due primarily to soil particles adhering to the lizard. Young lizards and lizards which had been washed did not change color to match a new background.

The coloration of the horned lizard also plays a part in the animal's ability to exert some control over its body temperature. Experiments have shown that the lizard is darker at low temperatures and at low light intensities and lighter at high temperatures and high light intensities (Atsatt, 1939). These chromatophores are subject to direct stimulation, nervous control, and hormonal control (Redfield, 1918; Parker, 1938). By coupling color changes with body positions the lizard can vary the amount of radiation which is absorbed or reflected.

CHAPTER III

ACTIVITY PERIOD AND THERMOREGULATORY BEHAVIOR

The activity of any poikilothermic animal is dependent upon its body temperature. The geographic range, seasonal activity, and daily activity of such an animal are a reflection of that animal's behavioral ability to keep its body within viable temperature tolerances. Each of these animals has a range of temperatures over which it is active and each has an optimum body temperature. Such animals depend upon a source in the external environment to supply the heat that will permit them to operate at maximum efficiency. The optimum body temperature for many poikilothermic animals is only a few degrees centigrade below the temperature which is lethal for that animal. Behavioral thermoregulation is most important in keeping the animal at an optimum body temperature but below a lethal temperature. The primary sources of heat for reptiles are the soil (Weese, 1917a; Cowles and Bogart, 1944) and solar radiation (Hutchison and Larimer, 1960). Behavioral responses to the heat received from these two sources are particularly important in the survival of desert animals (Cowles, 1939).

To obtain heat from the substratum a lizard simply moves onto and presses itself against a warm spot to absorb the heat radiating from it. The lizard lifts its body to a raised position or moves to a cooler spot in order to lose heat. The lizard's responses to solar radiation involve the coordination of several physiological and behavioral mechanisms. The cold lizard tries to orient its body at an angle of ninety degrees to the sun's rays and flattens out so that as much body surface as possible is exposed to the sun. The hot lizard orients its body to intercept as few of the sun's rays as possible. Physiological responses involve color, heat absorbing ability, and response to illumination. The cold lizard is of a darker shade and will become lighter in response to heat and illumination (Atsatt, 1939). Darker shades absorb more heat than lighter ones. This reaction is particularly noticeable in P. modestum which has a light colored body and can have black patches at the flanks and shoulders. Regardless of color, there is a differential heat absorbing capacity between the integuments of desert, semi-desert, and forest dwelling lizards, desert lizards absorbing the least and forest lizards the most heat (Hutchison and Larimer, 1960). The parietal eye of lizards influences the time spent exposed to high-intensity illumination (Stebbins and Eakin, 1958). Phrynosoma is among the lizards found to have a well developed parietal eye with a nervous connection to the habenular apparatus (Eakin and Stebbins, 1959).

The horned lizards exhibit definite thermoregulatory behavior and their daily activity is very markedly controlled by the temperature. All the species which I have observed exhibit a similar pattern of behavior in their daily activity. The description which follows might be considered "typical" of the activity of a Phrynosoma on a summer day in Oklahoma. The time involved in any component of the description will vary with the environmental conditions. The conditions may even be such that one or more components are omitted in the activity of the lizard on a particular day. An analysis of the relations of temperature to the various behavioral patterns in the activity cycle has not been attempted.

A Phrynosoma usually spends the night buried in loose soil or under some object such as a rock or log. As the lizard emerges from its place of concealment, the first part of the body to be exposed is the head. A cold lizard may remain with only the head exposed for some time before exposing the rest of its body. This type of behavior is common to many lizards. During a visit to our laboratory several years ago, Dr. Raymond Cowles suggested that blood collected in the large sinuses of the head is warmed in this way before being circulated to other parts of the body. Thus a lizard is able to raise its body temperature several degrees to the point where the lizard can be fairly active before it fully exposes itself to the view of predators. By first exposing the head, the lizard can detect danger sooner and react to it faster than it could if some other part of the body was exposed first. As the lizard becomes warmer it moves sluggishly onto an area that is exposed to the radiation of the sun. The body is flattened and pressed against the earth. Some effort is made to orient the body in such a way that the flattened surface intercepts the sun's rays at an angle of ninety degrees (Fig. 5). This position is the one which is most efficient in utilizing the energy received from the sun. This orientation is accomplished by moving onto a slope of suitable angle in the habitat or by tilting up one side of the flattened body. Evidence for the fact that tilting is a response to illumination comes from the observation in the experimental enclosures where a lizard will tilt toward the reflection of light from the enclosure wall. On one occasion a P. modestum in an indoor enclosure tilted alternately back and forth toward the weak sunlight coming through a window and toward the reflection of electric lights from the enclosure wall. As the lizard warms up, the body loses its extremely flattened shape and the front legs are extended. In the alert position the fore-legs are fully extended and the body is at an angle of 30-45 degrees to the surface of the ground. The lizard now begins to move about feeding and investigating its surroundings. When the lizard begins to get too warm it may stop and orient its body so that the least possible surface intercepts the sun's rays. It sometimes opens the mouth and pants for several seconds. Panting is one means of lowering the body temperature. This method is poorly developed in desert animals, probably because of the considerable moisture loss involved. As the day becomes hotter the lizard retreats to a spot of shade. If no shade is available or if the temperature in shady spots becomes too high, the Phrynosoma burrows under the surface. In burrowing, the horned lizard puts its head down, wiggles it back and forth, and at the same time pushes for-ward with its feet. When partially covered it completes the process by wiggling the body and tail back and forth until the loose earth completely covers the lizard. Many times a horned lizard will bury itself and then expose its head. A lizard that ventures from the shade onto a hot sur-face will lift the toes when it stops, resting only on the heels of its feet. Toe lifting was not apparent in many of my observations since the foot was buried in the soft sand of the enclosure.

During the middle of the day there is a quiescent period, with activity reviving in the late afternoon and continuing until dark. Phrynosoma does not appear to be active at night ordinarily (Williams, 1959). However, I sometimes suspended a light over the enclosure at night to attract insects and on these occasions a few lizards remained active as long as the light remained on.

The yearly activity cycle of Phrynosoma can be described only in very general terms. During the winter they hibernate in the soil. Data on hibernation are almost completely lacking. P. m'calli has been found hibernating at a depth of twelve inches and a body temperature of 16.1 degrees centigrade, one degree above the soil temperature (Cowles, 1941). Hibernating individuals of P. cornutum have been found at a depth of about eight inches (C. C. Carpenter, unpublished notes). Horned lizards begin to emerge with the first warm days of spring and are active until the weather begins to turn cool in the fall. In many areas there is a burst of activity in the spring when the lizards are very noticeable and then a marked decrease in both activity and apparent numbers of individuals. It has been suggested that aestivation may account for this (Cowles and Bogart, 1936), but no evidence of aestivation has been found. From the observation of activity in my enclosures I can suggest that this may be due to a very short period of early morning and late afternoon activity on the part of the horned lizards as the days become warmer. In mid-summer the horned lizard will often have completed its morning activity period and will be retiring to shaded concealment by the time other iguanids are beginning to become active.

During the summers of 1961 and 1962 data was collected on a number of aspects related to the activity cycle of Phrynosoma. Daily activity periods are highly dependent upon the weather. Attempts to correlate activity with the time of day are therefore merely reflections of the temperature and insolation of a given time period. Attempts to correlate activity with temperatures other than body temperatures lead only to broad generalizations which have little meaning.

I was able to obtain a number of body temperatures from *P. platyrhinos*, *P. modestum*, *P. coronatum*, and *P. cornutum* living in my enclosures. Temperatures were taken with a quick-reading Schulthesis Reptile Thermometer inserted into the cloaca. A record was also kept of the activity of the lizard immediately prior to capture. Sometimes a lizard was caught by hand but the usual method of capture was the noosing technique. The temperature was taken immediately after capture. An effort was made to obtain temperatures at all periods when the lizards were visible. Temperatures immediately after emergence in the morning ranged from 18.2 - 25.0 degrees centigrade and were within one degree of the soil temperature. On a typical summer morning the lizard's temperature had risen to above 30 degrees centigrade within 15-30 minutes after emergence.

I regret that no comparable data are available for *P. douglassi*. All of the specimens that I have had during my study have exhibited less tolerance for heat than other horned lizards. When placed in an enclosure they rarely ventured out of the shade and their health steadily waned. The only way they could be kept at all was to place them in a shaded cage which was so situated as to catch the maximum available breeze.

The information obtained in this study is summarized in Table 1. The thermal activity range for the four species studied can be obtained by consulting this table. Though I noted active lizards at or near the highest recorded temperature for each species, I feel that the optimum temperature for these species lies somewhere near the average for active temperatures.

TABLE 1

SUMMARY OF CLOACAL TEMPERATURE RECORDS OF PHRYNOSOMA

Species	Temp. °C. of Active Lizards				All Available Lizard Temp. °C.			
	No.	Low	High	Avg.	No.	Low	High	Avg.
P. platyrhinos	24	23.2	38.4	32.89	109	20.2	40.6	34.48
P. modestum	41	24.4	38.2	32.75	88	18.2	38.2	33.19
P. coronatum	38	24.0	40.4	34.52	98	19.8	40.4	34.18
P. cornutum	87	23.8	39.8	34.82	143	16.6	41.2	34.41

Other studies which have included temperature records of P. coronatum, P. platyrhinos, and P. m'calli (Cowles and Bogart, 1944; Norris, 1949) have indicated a slightly higher (2-4 degrees centigrade) activity temperature for these species. Examination of the conditions under which the various studies were made reveals a possible explanation for the discrepancies in results. Both of these studies base their estimates of activity temperature on fewer observations, with narrower extremes, than I have used in my own study. Norris obtained data from P. m'calli which were flushed from retreats and chased over the hot sand before the temperature was read. Cowles and Bogart set up cages and enclosures on the open desert and studied all the species mentioned above. The small amount of shade available in the enclosures was provided by a large pipe half buried in the sand and by small squares of "Cellotex" placed 250 mm. above the ground. In this study the upper limit of activity was the temperature at which the lizard buried itself or moved into the small amount of available shade. In my enclosures a large amount of shade provided by thick grass and sunflower plants was readily available. My lizards would retreat to the shade rather early in the day and remained inactive until late in the afternoon. Thus the cloacal temperatures that I recorded from active lizards reflected a lower preferred body temperature than that seen in the earlier studies.

In subsequent work Bogart (1949) has found that lizards whose activity in open sun is prolonged may reach temperatures in the upper limits of their activity range. He found that lizards rarely remain in the open or on a hot substrate until their limit of voluntary tolerance was reached but ordinarily sought a cooler spot whose temperature approximates the mean of the normal activity range. In his comparative temperature work Bogart has found that closely related forms tend to have close thermal preferences even though they are widely separated geographically and to some extent ecologically.

CHAPTER IV

REPRODUCTIVE BEHAVIOR

A review of reproductive behavior and associated aspects of the life history of the genus *Phrynosoma* is interesting, challenging, and frustrating. The extensive literature, reviewed by Milne and Milne (1950), consists of isolated bits and pieces that when fitted together leave large holes in the picture of this animal's life. Recent literature has done little to fill the gaps indicated by the Milnes. The account which follows is drawn primarily from my own observations and merely confirms or duplicates much of what has been reported by others. I regret to admit that most of the holes in our picture of the life history of *Phrynosoma* remain unfilled. Data on the subjects of growth rate, age of breeding individuals, number of broods per year, population density, and longevity are practically non-existent.

Breeding activity seems to begin as soon as the lizards emerge from hibernation in the spring and may continue at least until mid-June. Most iguanids exhibit a definite courtship behavior consisting of preliminary challenges by means of the characteristic head bobbing or push-up display of the species followed by a rapid head nodding as the male approaches the female. The six accounts of copulation in *Phrynosoma* in the literature do not mention any courtship activity. I have witnessed very little that might be interpreted as courtship among the horned lizards. On one occasion a male _P. coronatum_ approached a female from the rear and was seen to give a few rapid nods. The female moved to one side, looked back at the male, and then they went their separate ways. On several occasions male _P. cornutum_, _P. modestum_, and _P. platyrhinos_ have slowly approached females and tested the femoral region with the tongue. In every case the female assumed a characteristic posture in which the fore part of the body is lowered, the hind-quarters raised, and the tail elevated (Fig. 7). This is apparently a rejection posture. If the male followed the female as she moved away, the posture became exaggerated and the male and female would soon go their separate ways.

Tail waving has been reported to serve as part of rejection behavior directed toward courting males by the females of _Leiocephalus_ (Noble and Bradley, 1933), _Sceloporus undulatus_ (Noble and Bradley, 1933; Carpenter, 1962a), _Sceloporus merriami_ (Carpenter, 1961b), and _Holbrookia_ and _Callisaurus_ (R. F. Clarke, personal communication). In all of these forms the display often passes quickly from a rejection phase to a phase of active aggression toward the male. The aggressive display involves the arching of the back and a "sidlehopping" movement as well as the waving of the tail.

On three occasions a male was seen to run to a female from a distance of several feet, grab her horns in his mouth, and begin attempts at copulation. A few other copulations were observed which involved little or no courtship activity. In these instances a lone female was observed, then a few minutes later a male was copulating or attempting copulation with her.

I have observed copulation or attempted copulation in _P. cornutum_, _P. modestum_, and _P. coronatum_. In the former two species the male grasps one of the occipital horns of the female in its mouth and hangs on determinedly as the female usually tries to escape. The male twists his pelvic region as far under the female as possible and inserts the hemipenis into the cloaca of the female. If the right horn of the female is gripped, the male usually slips to the right and the left hemipenis is used or _vice versa_. No attempt is made to turn the female onto her back and she may even crawl about during the copulation attempt. Several times I have seen females of _P. cornutum_ which exhibited a broken horn when the male released her after copulation. It is not unusual to find a female _P. cornutum_ with both occipital horns broken off, mere nubs indicating their former presence. (One such individual was the basis for the description of a new species.) In the one copulation attempt of _P. coronatum_ which I have witnessed, the male seemed to shift his grip on the female from the occipital horns, to the temporal horns, to the mandibular spines as he attempted to turn the female onto her back. When the female was finally on her back the male shifted his grip to the skin of the under side of the chin and held her immobile as the copulation proceeded. A similar performance was described by Wood (1936). This act of turning the female onto her back during copulation appears to be unique among lizards. Copulation attempts in the three species mentioned last from a few minutes up to at least half an hour.

I have observed one type of action on the part of gravid females which seems not to have been noted previously. When another lizard touches the back of a gravid female _Phrynosoma_, the female begins a stiff, rapid jerking of the body and especially the head. The tendency to do this seems to increase as the time for nesting draws nearer. This action seems to be very effective in discouraging a male who is attempting to secure a hold on the female and thus prevents copulation and the possible result of abortion of underdeveloped eggs.

In connection with the behavior studies conducted at the University of Oklahoma on iguanids it has been discovered that the gravid females of many species develop a distinctive coloration, usually of red or orange spots or blotches. The extent and intensity of this coloration increases as the eggs develop, reaching a high point just before nesting. Paralleling the development of this coloration is the development of aggressive behavior by the female toward other lizards which approach her. After nesting, the coloration and aggressiveness fade rapidly. No female Phrynosoma in my possession developed this type of coloration or behavior as her eggs developed. The jerking behavior described above has perhaps developed to serve the same purpose in this genus as the color and aggressive behavior serve in other genera, that is, to prevent copulation with females whose gravidity is well advanced.

It is well established now that all of the United States horned lizards lay eggs except P. douglassi which gives birth to living young. The interval of time between copulation and the laying of the eggs or birth of young is known in only a single case. Hewatt (1937) reported a forty-four day interval between copulation and egg laying in a female P. cornutum.

I have had nests dug in my enclosures by P. cornutum and P. modestum. The site was usually on a slope and most of the nests faced south. A tunnel slightly larger than the female's body was dug into the earth, descending at an angle of 25 - 45 degrees. This tunnel was 5 - 10 inches long and could be straight or could be curved to one side at the lower end. There was a slightly enlarged chamber at the lower end in which the eggs were deposited. The female dug with the forefeet and kicked the dirt out of the way with the hind feet. She would dig for several seconds then pause for a short time. As the female turned to the entrance at the beginning of the rest period she would sometimes use the forefeet and head to shove accumulated dirt out of the entrance. During the rest periods she would lie in the mouth of the tunnel and look around. After the eggs were laid the female began to kick dirt over them with her hind feet. As soon as a layer of dirt had accumulated the female would turn around and tamp it down with her forefeet and forehead. As the tunnel filled, the female would emerge and go as far as one and one-half feet away to kick dirt toward the tunnel entrance. When the tunnel had been filled the female continued to move dirt around the immediate area, scattering, sifting, and smoothing until all traces of activity had been removed. When she had finished, the spot where the eggs had been deposited was undetectable. The whole nesting process took 5 - 10 hours. A female often remained in the area of the nest for a few hours after its completion, even moving to another point of the enclosure and returning several times. However, after a few hours had passed no further interest in the area was noted. There was no evidence of parental care among these lizards. If a female was weak or if weather conditions were adverse at nesting time, the eggs were deposited on the surface or in a shallow depression which the female managed to scrape out of the soil. Such clutches were unsuccessful. _P. douglassi_ in our cages gave birth to young on the surface. The female moved about the available area during the time so that the young were scattered.

It may be pure coincidence, but all of the females which laid eggs or gave birth in our enclosures died a short time later. The only readily apparent explanation for this seems to be that in their weakened state they could not compete successfully for food in the enclosure. Whether or not this would occur in nature I cannot say.

Incubation time for the eggs varies with the summer weather. Clutches of P. cornutum and P. modestum which have been successful in our laboratory hatched 60 - 70 days after laying. Some of these were left undisturbed at the original nest site; others were dug up, measured, and incubated following the method described by Carpenter (1960). Two female P. douglassi gave birth in late July. Young horned lizards may be hatched or born any time between late July and early September. Within a few minutes of hatching or birth the young Phrynosoma runs about actively, though somewhat clumsily, feeds on small insects, and bobs its head in the manner characteristic of its species.

CHAPTER V

DISPLAY

One of the principal objectives of this investigation was the study of the display and associated social behavior. It was soon discovered that neither display nor social behavior is very highly developed in the forms of *Phrynosoma* observed.

The iguanid display functions in species recognition (Hunsacker, 1960), declaration of territory, challenge for social position, sex recognition, and perhaps courtship (Carpenter, 1962a). As indicated previously there is little or no courtship of any kind in the *Phrynosoma* I have studied and there is certainly little to indicate any use of the display in courtship. In the matter of sex recognition, both males and females perform the display with no apparent difference in situation, place, intensity, sequence, or cadence. I have seen no evidence of any type of a social hierarchy or of territoriality in *Phrynosoma*. This is the only group of iguanids studied thus far which is not known to exhibit these behavioral characteristics. It may function in species recognition, though I have run no tests such as those performed by Hunsacker. Actions of the lizards in the observation enclosures throw no light upon this question.

The horned lizard will display frequently when first introduced into a new enclosure or cage, but there is no indication that the display is directed at any other lizard or at any particular object. As one watches other sceloporines under similar conditions, one can learn to predict with a high degree of certainty when a display will be given by a lizard; but this is not the case with Phrynosoma. A newly introduced Phrynosoma may or may not display after every change in location as it moves about its new environment. The horned lizard may display when it sees another individual, but it is more likely that each will continue its activity with no sign of recognition of the presence of the other. Sometimes a display is given when a food item is seen or after eating. Sometimes a single display is given; at other times the display is repeated two or three times. As the period of captivity lengthens, especially if the place of confinement is small, the frequency with which the display is performed decreases.

There is no doubt that the iguanid display is a ritualized performance. However, the origin of the display is open to speculation at the present time. One hypothesis which has been advanced is that the display originated as an effort to improve the visual field or visual perception. This idea correlates with the apparent necessity for motion in the object perceived visually to which the lizard reacts. It is interesting to note that in its present stage of development the eyes are often shut during part of the display. Two other possible sources of origin for this display have occurred to me. The first is suggested by the action of P. douglassi immediately after birth. As the young lizard shakes its head and breaks the surrounding embryonic membranes, it gulps for air and as it gulps the head is tossed up. As the young lizard staggers about this gulping continues at irregular intervals.

Five to ten minutes after the young lizard is free of the embryonic membranes the gulping movements are no longer evident, but head bobbing in the manner characteristic of the species may be seen. Another possible origin for head bobbing movements was suggested to me by Carr's (1962) description of how young sea turtles emerge from the nest. They raise the cavity around them at hatching to the surface by knocking sand from the roof of the cavity and trampling it underneath them. If young lizards make their way to the surface in a similar manner, it may be that head movements are used in some way and have become secondarily ritualized into a display in the Iguanidae.

Carpenter (1962a) outlined eight characteristics to be considered in the analysis of an iguanid display: site, position, posture, movement type, parts moved, units of movement, sequence, and cadence. Information regarding the first five of these catagories is easily obtained by direct observation of the display. An analysis of the last three catagories becomes a bit more complicated however, and it is this aspect of the display which seems to hold the most promise for future investigation. A method of studying this aspect of the display through the use of stop-watch timings was outlined by Carpenter and Grubitz (1961) in a report on the display of Urosaurus ornatus.

In my study of the display of Phrynosoma, it soon became apparent that stop-watch timings were not adequate for the analysis of this rapid display. The whole display lasted only three-tenths to five-tenths of a second in most cases. This observer can barely operate the stop-watch within these limits and I held reservations as to the accuracy of many timings of the whole performance. Thus, attempts to time portions of the display manually were out of the question. It was decided that motion pictures of the display which could be viewed slowly and repeatedly would provide the best solution for this problem. During 1961 and 1962, 16 mm. motion pictures taken at sixteen frames per second were made of the displays of all the United States species of *Phrynosoma* except *P. m'calli*. Though this film speed has proved to be adequate, films taken at faster speeds would be desirable where it is practical to obtain them. It was possible to analyze these motion pictures frame by frame with the aid of a motion picture film editor which projected the picture on a small ground glass screen. Some motion pictures were obtained in which the wire screen of the cage was visible behind the lizard and thus provided a ready reference for measuring the movement of the head as the lizard displayed. However, many good films of displays were obtained which had no good background reference points. In conjunction with Mr. Robert F. Clarke, who is working on a similar problem with the genus *Holbrookia*, a method was worked out in which dividers were used to measure the distance between some point on the head and some other point on the film which was evident throughout the display. As each frame was viewed on the screen of the editor, the measurement was made and recorded. When a complete display had been studied in this way a tracing of the display could be plotted graphically. A tracing table was constructed with a permanently affixed ruled paper to serve as a guide. Each division on the horizontal axis represented one frame of the film. Each division of the vertical axis represented one unit of measurement. When several displays have been reconstructed in this way, they can be compared very easily. A rule was constructed which was calibrated in tenths of a second and scaled to the interval allowed for sixteen frames on the graph used as a base for the reconstruction. Using this instrument it was possible to measure the time involved in each unit of the display.

In my study of Phrynosoma I have seen them display hundreds of times, both in the field and in enclosures. Before the technique of motion picture analysis was developed, many hours were spent in trying to time the display with a stop-watch and in trying to determine the sequence of units and cadence of the display in the various species. Many of the concepts of form of the display developed in this way were confirmed by the study of the motion pictures as outlined above. Of more importance perhaps is the fact that study of the film has also revealed relationships between units of movement, sequence, and cadence which did not register with the observer at first, but which are readily apparent in subsequent observation of the displaying lizard. The representations of the display illustrated in Fig. 17 are a composite of information obtained by the analysis of the motion pictures.

Following Carpenter's eight catagories the display of Phrynosoma is described as follows:

1. Site: No particular site is utilized. The lizard will display wherever it happens to be.
2. Position: No particular body position is assumed during display except that the lizard is stationary during the display. The usual body position for an active or alert horned lizard has the fore part of the body raised at about a thirty degree angle with the ground. This is the position in which most displays are performed. Displays may be given by horned lizards lying down with only the head raised. An occasional display has been seen performed by a lizard with

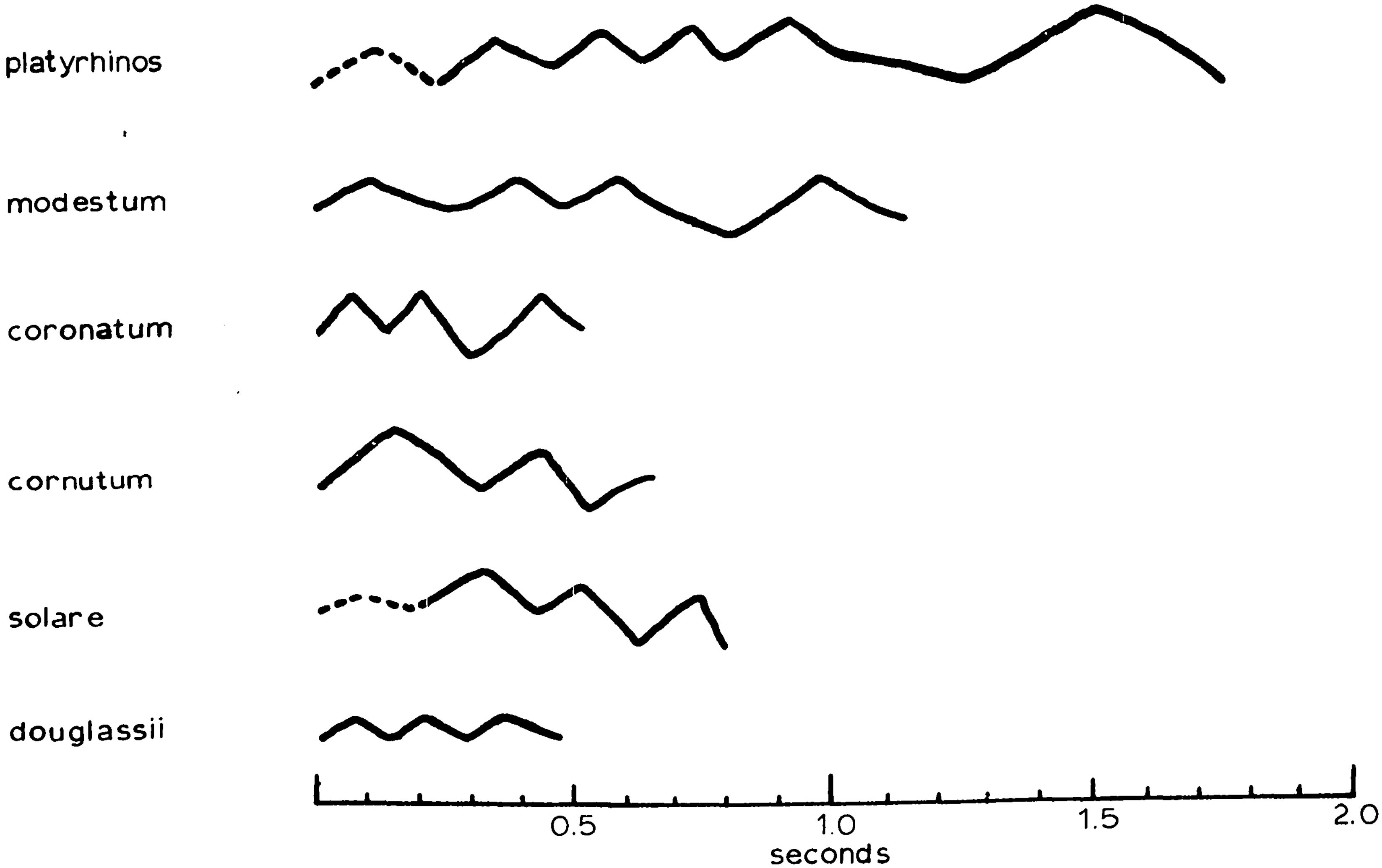

Fig. 17.--Display action pattern graphs for the Phrynosoma species studied. Dashes = units present in about one-half of displays studied.

only its head exposed above the surface of the ground. There is no orientation toward a possible recipient of the display.

3. Posture: No change in posture was associated with the display. Phrynosoma has no ventro-lateral coloring as do other sceloporines and the body is not compressed in display as it is in those forms which flash their brilliant coloring during display.

4. Movement type: Display in the iguanids has long been labeled simply head bobbing. Analysis of displays in our laboratory has revealed that the display often involves more than this simple movement. At least three basic types of movement are present in the family: head bob, push-up, and an upward stretch of the whole body. The display of the horned lizards is a head bob.

5. Parts moved: Only the head is moved in the horned lizard display. No other portion of the body is involved in the bobbing motion unless the display is extremely intense in which case the fore part of the body may become involved.

6. Units of movement: The unit of movement in the Phrynosoma display is a simple up and down movement of the head in the vertical plane.

7. Sequence: The sequence of units in the species studied is as follows:

   Phrynosoma platyrhinos: Three (sometimes four) quick bobs, a bob with quick upward movement and a slow downward movement, a slow bob.

   Phrynosoma modestum: Two quick bobs, a bob whose downward movement is lengthened, a slightly slower bob.

Phrynosoma coronatum: Three quick bobs of high amplitude.

Phrynosoma cornutum: Two and a half quick bobs of gradually decreasing amplitude.

Phrynosoma solare: Three (sometimes four) quick bobs.

Phrynosoma douglassi: Three very fast and very low amplitude bobs.

8. *Cadence*: The time required for each unit varies somewhat with the individual and the situation but is relatively constant within a species (Table 2). The times indicated in the display action pattern graph (Fig. 17) are averages of several displays for each species. Each time the display is given it is a complete performance (unless interrupted by some outside influence). The display may be repeated after a short pause, but there is no continuous repetition as is evident in some other species of iguanids.

As we look at the representations of the display patterns in *Phrynosoma*, it is readily apparent that the pattern for each species is specific to that species. It is also evident that there is very little difference between several forms, the display having the same number of units but varying in the time required for each unit and in the amplitude of the units. The displays of *P. coronatum* and *P. douglassi* are both composed of three units and the total time involved is very nearly the same. However, the display of *P. coronatum* always involves considerable movement of the head, while that of *P. douglassi* is of such a low amplitude as to be barely discernible to the observer.

In its function as a species recognition signal there is the possibility that the similarity of the display in *P. coronatum* and

TABLE 2

SUMMARY OF UNITS OF MOVEMENT, SEQUENCE, AND CADENCE OF DISPLAY PATTERNS OF *PHRYNOSOMA* AS DETERMINED BY MOVING PICTURE ANALYSIS

Species	Units in Sequence	No. of Timings	Range (sec)	Mean (sec)
P. platyrhinos	1	5	0.18-0.26	0.232
	2	6	0.16-0.25	0.212
	3	15	0.12-0.25	0.180
	4	17	0.11-0.19	0.162
	5	16	0.31-0.65	0.437
	6	13	0.35-0.57	0.492
P. modestum	1	7	0.18-0.31	0.267
	2	7	0.12-0.26	0.186
	3	7	0.18-0.41	0.342
	4	7	0.25-0.50	0.345
P. coronatum	1	10	0.11-0.18	0.131
	2	11	0.13-0.18	0.169
	3	10	0.15-0.28	0.201
P. cornutum	1	24	0.18-0.38	0.319
	2	23	0.11-0.28	0.207
	3	22	0.08-0.28	0.128
P. solare	1	5	0.180	0.180
	2	9	0.18-0.31	0.240
	3	9	0.13-0.25	0.182
	4	9	0.11-0.25	0.161
P. douglassi	1	11	0.11-0.18	0.131
	2	11	0.11-0.25	0.137
	3	10	0.11-0.25	0.187

P. douglassi might lead to interaction between the species if this were the only factor separating them. However, these two species are allopatric. If we compare the geographic ranges of the species and the display patterns of the species, we find no two sympatric species with similar display patterns.

When we compare the phylogenetic tree proposed by Reeve (Fig. 4) with the display patterns (Fig. 17) certain correlations and implications can be seen. *P. platyrhinos*, the most primitive form, has the longest and most involved display. *P. modestum*, which is very closely related, has a somewhat simpler and slightly shorter display. The more advanced forms have increasingly shorter and simpler displays and the similarity in the displays agrees with the taxonomic closeness indicated by morphological studies. It will be very interesting to see how the displays of the other forms of this genus fit into this picture.

CHAPTER VI

DISCUSSION

The objectives in this study have been to describe various aspects of the behavior of the members of the genus *Phrynosoma*, to compare the species studied, and to assess the value of the results obtained to taxonomic and evolutionary studies.

This is by no means a new approach, but one whose possibilities are just beginning to be utilized extensively. Whitman (1899) as long ago as 1898 said "instincts, like corporeal structures, may be said to have a phylogeny. ...The main reliance in getting at the phyletic history must be comparative study." After a thirty year dormancy this idea was revived by the studies of Lorenz, Tinbergen, and their students. It is now part of the philosophy underlying studies by many investigators.

Behavioral characteristics, like morphological characteristics, express themselves at the various taxonomic levels. Species specific behavior patterns are most likely to express themselves in courtship or threat displays. Other behavioral patterns may be limited to a subfamily or larger taxonomic group (Tinbergen, 1960; Andrew, 1956).

Comparative behavioral evidence is becoming increasingly more significant in taxonomic studies. When evaluated in the same manner as other criteria, it often reveals relationships that were heretofore overlooked. In many of these cases subsequent re-investigation of the morphological evidence has confirmed the relationships indicated by the behavioral evidence (Mayr, 1958). In studying evolution, the behavior student can only utilize comparisons between living forms. Hinde and Tinbergen (1958) have outlined factors to be considered in such a study.

Studies in the evolution of behavior seem to have pointed in two directions in the past. The most intensively studied area endeavors to trace the evolution of particular displays from their origin to their present form. This is particularly illustrated in the several studies of birds by Tinbergen, Hinde, Andrew and others. The other direction is the attempt to trace the development of a behavior pattern within a taxonomic group. Davis (1942) traced the evolution of social nesting in the Crotophaginae; Winn (1958) traced the evolution of spawning habits in darters; and Dilger (1960) has traced the evolution of reproductive behavior patterns in parrots of the genus Agapornis.

As I reviewed the literature in preparing this discussion, I found two workers who have introduced ideas which I had been developing concerning the evolution of behavior in Phrynosoma. The first is that changes in a behavior pattern can be correlated with the ecology of the animal, as is shown by Cullen's (1957) work with the kittiwake. The second is that..."since characters of courtship are causally and functionally related to characters used in other situations they may diverge in isolated populations without selection for divergence. Such changes are especially likely to be related to changes in aggressiveness and timidity, sexual dimorphism and color. Divergence in this way is likely to be significant in providing a basis for divergence in sympatric forms" (Hinde, 1959).

If one were to arrange an exhibit of specimens of the family Iguanidae, one of the very striking points apparent to an observer would be the distinct divergence in physical appearance from other members, especially other North American forms, by the genus Phrynosoma. The development of horns on the head is a very distinctive feature. Further examination would leave the impression of a short, depressed body and short toes as contrasted to the longer, slimmer appearing bodies and longer toes of other forms. These characters seem to indicate that, at least morphologically, here is a distinct sideline in the phylogeny of the iguanids (Figs. 1, 2, 3).

Behavior patterns among the Iguanidae are poorly known thus far. Only a few species and fewer genera have been studied at all from the standpoint of social behavior: Anolis - Evans, 1936, 1938; Greenberg and Noble, 1942, 1944; Sceloporus - Noble and Bradley, 1933; Carpenter, 1961b, 1962a; Hunsacker, 1960; Dipsosaurus - Carpenter, 1961a: Urosaurus - Carpenter and Grubitz, 1960: Ctenosaura - Evans, 1951. Only two studies have tried to make behavioral comparisons within a supposed taxonomic unit (Hunsacker, 1960; Carpenter, 1962b). Several studies of this nature are now being made at the University of Oklahoma.

A summary of what is known about iguanid behavior reveals that the family is very homogenous. The use of the senses does not seem to vary appreciably from that described for Phrynosoma on preceeding pages. Feeding behavior varies with the size, smaller forms being more active and insectivorus, larger forms being slower and relying on plants for food though insects are eaten also. All forms use behavioral thermoregulation in essentially the same manner as described for Phrynosoma.

Information on preferred body temperatures is yet too meager to be of any comparative value. There are a variety of defense reactions, such as making use of the special development of the tail (whipping in Iguana and Urocentron, autotomy in many forms), protective coloration, and puffing up to wedge the body tightly in a crevice as does Sauromalus. The principal means of defense in all forms is a quick retreat. Courtship nodding and copulation positions are similar in most forms. All forms studied thus far, except Phrynosoma, are highly territorial. If several individuals of a species are limited to a small area, a dominance hierarchy is formed. All forms that have been studied have some type of display. During the display many forms compress the body to make it appear larger and at the same time show off any coloration that may be present. Three basic types of movement have been noted in the display. Some groups use only a head bob, others a push-up, and others an upward stretch of the entire body. The function of this display is the intimidation of nearby lizards. The display has thus far proven to be species specific.

Comparison of the genus Phrynosoma with other iguanids reveals that its behavior differs radically from that of other members of the family in one important aspect. This is in the area of social behavior. While it still performs a display, the display is relatively weak and seems to no longer serve the function it does in other iguanids. There is no evidence of territoriality or dominance. There is little or no courtship.

The question now arises as to why the genus Phrynosoma should be different from other iguanids in this particular aspect of its behavior. The answer to this question is highly speculative and I do not feel warranted in doing more than suggesting a possibility or two.

Let us review what we know about these lizards. They are an old group in relation to other North American iguanids. They apparently originated in the Sonoran Desert and in their spread from that area have remained essentially desert or semi-desert forms. The species which are presently undergoing differentiation are those that are invading new habitats. In morphological and defensive behavioral characters this lizard is highly specialized for a habitat providing little opportunity for active escape from predators. In this regard lack of elaborate coloration and display can be correlated with inconspicuousness. The horns and blood squirting are unique defensive developments in an animal which has little or no chance to retreat once it is discovered by a predator. Little is known of the population structure of this genus, but apparently the populations are widely scattered and each contains relatively few individuals. Only a few instances are known where these lizards have been found in any concentration of more than a few individuals. If this picture of the population structure is true, it would seem that the characteristic of territoriality might serve as much to inhibit successful propagation of this form as the inverse is true in other forms. Correlated with this may be the lack of a courtship display.

In a consideration of behavior within the genus Phrynosoma, we find that these lizards are similar in most respects. There may be some slight differences in courtship behavior but not enough is known to make any statement in this regard at the present. Differences in behavior during copulation have not been satisfactorily described and the differences that do exist, or apparently exist, can be correlated with the morphology. One difference that is noticeable in the studies undertaken thus far is in the divergence of the display. The display varies in extent of development, in time per unit, and in the amplitude of the units. Arranging the display patterns in the phylogenetic sequence for the species proposed by Reeve (1952), we find that there is a definite trend from a more complex display in the more primitive forms to a simpler display in the more advanced forms. This trend toward simplicity is accomplished by the elimination of elements in the display, by the shortening of the time for a particular unit, and by a change in the amplitude of the display.

Since the display is one aspect of the behavior of the horned lizards which is species specific, the question arises as to its role as an isolating mechanism. A comparison of the distribution maps shows that all of the United States species are sympatric with at least one other, and often more, species over a part of their range. Undoubtedly the differences in display do have some role in keeping the species from interacting. The species recognition role of the display as developed by Hunsacker (1960) would serve this purpose. It is difficult to answer the question of whether or not these displays evolved as isolating mechanisms or are the result of genetic drift within populations of the genus and have secondarily assumed the role of an isolating mechanism. After reviewing the history of the genus as presented by Reeve (1952), I am inclined to accept the latter view. Reeve has described the probable radiation of Phrynosoma from the place of origin in the Sonoran Desert. This radiation took place in three waves. In the first wave P. m'calli went to the west, P. platyrhinos went to the north and has since pushed southward again, and P. modestum went east and northeast. I have described the display of the latter two species. These two species have somewhat similar displays, that of P. platyrhinos having a few more units. At the present these two have allopatric distributions. The second wave from the center of origin included P. solare, which remained in the Sonoran Desert; P. cornutum, which moved east and northeast; and P. coronatum, which went west and then south. The displays of these three species are quite similar, varying principally in the time element. These displays all have fewer units than those of the more primitive forms. P. solare and P. cornutum are sympatric over a very small portion of their ranges, but these three species are primarily allopatric. The last wave of dispersal includes P. douglassi. This form has a very short and simple display. The display of P. douglassi is very distinct from that of the several species with which it is sympatric. The cadence of its display most closely resembles that of P. coronatum, an allopatric species.

Each of the waves of dispersal had Mexican components, but the displays of these species have not yet been studied. I expect that these forms will prove to have display patterns which will fill in gaps in the present display pattern picture to the point where we can go from one species to the next with a change in number of units, sequence, and finally just changes in cadence and amplitude.

The similarity of the displays among the members of each of the various waves of emigration from the center of origin leads me to think that the specificity of the displays has arisen as the result of genetic drift within the populations resulting from each wave of emigration. The species recognition function along with other factors is sufficiently strong to prevent interaction with species which are sympatric as a result of some other wave and thus display serves as part of the isolating machinery. The fact that species with very similar displays are allopatric prevents any possible breakdown of the recognition function of the display and resulting hybridization.

We might conclude from the above that the genus Phrynosoma in its present ecological circumstances is losing some of the behavior patterns evident in other iguanids because those patterns play no part in selection for survival and/or it may be that they are even selected against for their inhibition of survival of the species.

SUMMARY

The behavior of the United States forms of the genus Phrynosoma is described and comparisons are made within the genus and with the family Iguanidae. Attempts are made to show how behavior can be correlated with ecology and to show how behavior can be useful in taxonomic and evolutionary studies.

The sense of vision appears to be the most important sense in determining behavioral actions among the horned lizards. The chemical sense may be important in sex and species recognition but its role is not clear at the present time.

Horned lizards will ingest any object of appropriate size which meets the prerequisite of motion, yet is slow enough to be caught. Agricultural ants are the preferred food. Defecation is performed in the typical iguanid manner.

Defensive behavior has two phases. The first is to escape detection. The horned lizard will retreat to cover if it can. Protective coloration is highly developed and the immobile lizard is extremely hard to detect. The second phase is to discourage the predator if the lizard is molested. If the horned lizard is picked up, the horns are used to induce release. At times blood may be squirted from the eyes to startle the predator. The last thing the horned lizard does is to puff up and stiffen itself, becoming hard to swallow.

The horned lizards maintain themselves near their optimum temperature by means of behavioral thermoregulation. Body temperature is controlled by the angle of exposure of the body to solar radiation and by movement onto areas of the substratum which are of appropriate temperature. Characteristics of the integument and chromatophores also play a part in temperature regulation. Preferred body temperatures for four species have been determined: P. platyrhinos - 32.9, P. modestum - 32.8, P. coronatum - 34.5, and P. cornutum - 34.8 degrees centigrade.

The horned lizards exhibit little, if any, behavior which can be interpreted as courtship. The usual case seems to be for the male to rush to the female, grasp one of her occipital horns in his mouth, twist his cloaca under the female, and insert the hemipenis into her cloaca. P. coronatum turned the female on her back and transferred its grip to the skin of the chin during the one copulation recorded for this species. Copulation has not been observed in the majority of species. Eggs of P. cornutum and P. modestum laid in Oklahoma hatched in 60-70 days. All females which laid eggs in the study enclosures died a short time afterwards.

No evidence of territoriality or dominance was seen in Phrynosoma. Display is still performed by Phrynosoma but has apparently lost many of the functions it serves in other iguanids. The display for all of the United States species except P. m'calli is described and display action pattern graphs are presented for comparison.

Within the genus Phrynosoma there is an apparent evolutionary movement away from the performance of a display. Primitive forms have more complex displays; recent forms have simpler displays. The general complexity of the display and differences between allopatric and sympatric species can be correlated with the morphological and zoogeographical evidence for waves of emigration from the center of origin of the species.

It is suggested that the ecology of *Phrynosoma* is such that the behavior patterns of territoriality, dominance, and elaborate courtship are not beneficial to this genus as they are to other iguanids. Display is a part of the structure involved in these behavior patterns. Thus, as these behavior patterns are lost during the course of evolution, display patterns are also being modified in the direction of elimination.

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