

A PRELIMINARY STUDY OF THE THERMAL REQUIREMENTS OF DESERT REPTILES

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INTRODUCTION

AT THE PRESENT TIME there is little available information on the influence that desert climates exert on ectotherm activities. The small amount of data which are available has been gathered chiefly as matter incidental to other problems in the biology of reptiles. Even with this meager information, the potential significance of these data requires more elaborate studies than those now available. It appears probable that temperature as a factor of the environment has a profound influence on reptilian distribution and ecology. Undoubtedly it has been fully as important in the evolution and dispersal of reptiles.

The great advantage inherent in studies of desert reptiles lies in the extraordinarily high maximum temperatures, as well as the greatly exaggerated temperature changes, so characteristic of desert climates. Such environmental conditions may amplify subtle details of thermal relationships that would otherwise escape notice. The resulting accentuation of temperature responses throws into relief temperature relations which in the equable climate of the tropics might otherwise remain as imperceptible, or at least unperceived, nuances in thermal adaptations.

Prior to undertaking the research reported here, it was believed that two types of investigations, (1) field studies and (2) laboratory experiments, would be necessary in order to obtain a general picture of the basic phases of the reptilian thermal problem. It was decided that the first effort should be devoted to field studies, and that it should be essentially observational rather than experimental in character. It seemed desirable that laboratory experimentation be held in abeyance pending completion of field work. Preliminary field study was designed with the express intention of observing the reactions of reptiles to the various temperature conditions that are encountered during the different seasons of the year, as well as those that are characteristic of the diurnal-nocturnal fluctuations. The results of these observations, and a few supplementary laboratory investigations required to interpret them, furnish the substance of this report.

Although it would appear to be a simple

matter to observe the activities of reptiles and to correlate these with temperature effects, it was learned that the task was by no means lacking in complications. One difficulty results from the presence of the observer within range of the animal's vision. It was soon discovered that an animal whose voluntary, unmodified reactions were desired either sought shelter before normal temperatures could have been attained, or it might prolong its exposure beyond normal limits due to the exceptionally strong stimulus resulting from the presence of "danger" as represented by the observer. In either case there were frequently no means by which the validity of observations could be determined, and in many instances it was necessary to resort to other techniques.

Eventually it was found that captive animals confined in open cages gave more satisfactory clues to behavior and consequently provided more satisfactory data than uncaged animals. In order to obtain good results it was necessary to allow the animals sufficient time in which to become adjusted to new surroundings. It also proved essential that they be replaced by a more or less constant flow of fresh material. Whenever possible, data assembled from caged animals have been compared with those obtained from occasional instances where wild, that is, unconfined, individuals have yielded apparently valid information. In both types of observations it was necessary to use caution in determining the validity of data. Only through experience can the necessary judgment be developed, and much of the information assembled when these investigations were first undertaken subsequently was discarded as being unsatisfactory.

The following reports on temperature relationships of reptiles are by no means complete or final. Pending more laboratory work, we have endeavored to include information on the salient features of temperature relationships of desert reptiles in so far as these are expressed by the animal's reactions to heat encountered in nature. The present paper is intended to serve as a survey of the field and for the presentation of results thus far obtained.

ACKNOWLEDGMENTS

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REVIEW OF THE LITERATURE

Several writers have called attention to the fact that reptiles as a group are not the highly thermophilic animals they were formerly believed to be. Nevertheless there is still a persistent tendency to think of them in terms of high temperature preferences. As recently as 1936 it is stated that "the temperature preferred by most reptiles appears to be considerably higher than is normally found in their environment" (Warden, Jenkins, and Warner, 1936, p. 141). Presumably the basis for such statements lies in the fact that reptiles often bask at marginal thermal levels near the minimum voluntarily tolerated. Or the "environment" may have been loosely thought of as consisting principally of the air. It is quite true that basking lizards often have body temperatures higher than those of the surrounding air, but Weese (1917) pointed out several years ago that substratum temperatures are far more important as factors of the environment. Furthermore, Weese found that the optimum substratum temperature was rather definite in the horned lizard, *Phrynosoma modestum*, between 36° and 40° C. "and at the upper limit a very definite reaction (burrowing) takes place."

Weese's observation closely corresponds to that of Kammerer (1926, p. 139) who found that lizards of the family Lacertidae were unable to withstand prolonged exposures to temperatures of about 40° C. In contrast are the findings of Herter (1941) for lizards of another family (Agamidae). After what appears to have been a careful investigation of voluntarily selected temperatures of these lizards, he states that the optimum or "V.T." of the Egyptian sand lizard, *Agama stellio*, is $45.59 \pm 0.3^\circ$ C. This figure seems astonishingly high in view of the fact this temperature approaches or exceeds the lethal temperatures reported for representatives of many metazoan groups.

Baldwin (1925) reports that aquatic turtles showed signs of acute discomfort at temperatures of 80° F. (26.5° C.) and that prolonged exposures to temperatures of 102° to 105° F. (approximately 39° to 40.5° C.) commonly proved fatal. Less conclusive but none the less instructive were the experiments reported by Reese (1923, p. 51) who provided juvenile alligators with a choice of three pans of water at approximate temperatures of 10° C., 25° C., and 40° C., respectively. He found that under such conditions alligators manifest a distinct preference for water at 25° C. with less liking for water at 40° C. and still less for water at 10° C. With the limited number of choices, however, it is improbable that 25° C. represents the optimum for this crocodilian; in all likelihood it is somewhere between 25° C. and 40° C.

Although optimum temperatures for vertebrates are perhaps of greater ecological importance than lethal temperatures, many more investigations appear to have been devoted to the latter than to the former. With improved observational techniques and better apparatus, however, the general trend has been to disregard some of the older records for lethal temperatures. Davenport and Castle (1896) reviewed much of the older literature and quite properly found it difficult to believe that fish on the island of Luzon survived temperatures of 86° C., as reported by Sonnerat in 1774 (it is possible that this represents a *lapsus calami* for a Fahrenheit record). Nearly as incredible, in light of recent findings, is the statement of Norman (1931, p. 291) that a small fish (*Tilapia*)

seems to thrive equally well in hot springs "ranging from 80° F. to 120° F.," or roughly 26.5° to 49° C. Kanitz (1925) apparently accepted no temperature tolerance reported for vertebrates that exceeded 45° C. Parker (1935, p. 139), in close agreement, states that the highest temperature at which multicellular life is known to exist is 45° to 48° C. reported for the crustacean, *Thermosbaena*. For birds the lethal temperature for adults has been determined by Baldwin and Ken-deigh (1932) with some precision as 46.8° C.

Nevertheless there is a persistent tendency to think of reptiles in terms of temperatures exceeding these. Even as late as 1937 (Hesse, Allee, and Schmidt, p. 14) it is stated "temperatures tolerated by desert insects and desert lizards correspond closely to those endured by animals of hot springs." Since these same authors state that the temperature range frequented by hot spring Metazoa extends to 45° C. (the Protozoa to 54.4° C.), it is clearly implied that desert lizards can tolerate temperatures of 45° C. and above. In view of the fact that air temperatures in desert regions inhabited by lizards are known to reach the maximum of 55° C., with the substratum considerably hotter, it would still be necessary to account for the existence of reptiles in such regions. Contrary to the statement quoted above, namely, that reptiles prefer temperatures "considerably higher than is normally found in their environment," one of the pertinent questions that might be asked would seem to be: How do reptiles manage to survive in environments where temperatures sometimes exceed the upper lethal limits known for these and other vertebrates? Obviously there are a limited number of possibilities: (1) reptiles can survive at such temperatures, (2) they are provided with some physiological means of cooling their bodies, or (3) they are able to avoid high temperatures by other means. In connection with the first possibility it is of importance to ascertain the lethal temperatures of reptiles living in desert regions.

Mosauer and Lazier (1933), in the first known technical report on temperature tolerance of desert reptiles, conclude that the diamondback rattlesnake, *Crotalus atrox*, and the sidewinder rattlesnake, *Crotalus cerastes*, cannot survive a body temperature above

46° C. While this information was obtained by the use of only three specimens (actual average for the three was 46.7° C.), their conclusions were supported by later studies. Mosauer (1936) states that under laboratory conditions the fringe-footed sand lizard, *Uma notata* (probably *U. scoparia*, vide Heifetz, 1941) and *Crotalus cerastes* died at 45° C., and that under field conditions "*Uma notata*" and *Callisaurus ventralis gabbii* (= *Callisaurus draconoides gabbii*) were killed at 47° and 47.5° C., respectively. It is probable that Mosauer's highest temperature records may be somewhat too high due to faulty criteria for death. Nevertheless Cole (1943) calls attention to the fact that his averages for lethal temperatures, as well as those obtained by Mosauer (1936) and by Cowles (1943) for the critical maxima, are all in close agreement. Together these investigators report lethal temperatures which average approximately 46.6° C. While some revision of this figure will probably be necessary, it is safe to conclude that our desert reptiles are not notably thermophilic.

That *Agama stellio* should have an optimum temperature virtually identical with the lethal temperatures of our desert reptiles seems highly improbable. The climate of north Africa and that of the deserts of the southwestern United States are strikingly similar, and these regions include the hottest known areas of the globe, both with known maxima of 55° C. While it is possible that *Agama stellio* has evolved an optimum temperature equal to, or actually above, the lethal point for our desert lizards, it seems more probable that some error in technique may explain this apparent anomaly. Consequently it would seem desirable to verify Herter's work on *Agama stellio*, as it is scarcely to be expected that any lizard from desert areas of north Africa, or from the southwestern United States, or comparable deserts of Australia and south Africa would be likely to develop such high optima or even a greater maximum toleration of high temperatures. Equatorial climates would not favor high temperature tolerance, since they are mild in comparison to the remarkably high maximum temperatures encountered between the latitudes 30° and 40° north or south of the equator. Maximum temperatures of the tropics

very seldom exceed 41° C., and the mean is close to 28° or 30° C.

Mosauer (1936) concluded from his experiments that there is little if any difference between the temperature tolerance of snakes and lizards, or between that of diurnal and nocturnal reptiles. Our data, as will be seen later, are not in accord with this conclusion.

One of the thermal problems meriting especial attention is that of the optimum temperatures of reptiles. This should be particularly interesting to herpetologists and ecologists of the southwestern United States where the extremes of a desert climate and the proximity of high mountain masses provide climates extending from Lower Sonoran to Boreal, as on the desert slope of Mount San Jacinto (pl. 19), where all these zones are crowded into the extraordinarily narrow air-line distance of 3 miles (Grinnell and Swarth, 1913). The faunas of one zone are often rather sharply delimited from those of the adjacent life zones in the Southwest, and optimum temperatures are presumably an important factor in the zonal preferences of many animals and plants. Verification of this view is suggested by the correlation which exists between altitudinal and latitudinal distributions of the reptiles of the Mount San Jacinto region (Bogert, 1939).

Mosauer (1936) designed an apparatus in which lizards were allowed to select their own temperatures and found that "*Uma notata*" came to rest at temperatures varying from 35°–40° C. with an average of 37° C. His field observations indicated the possibility of there being a slightly higher range of preferences, 37°–43° C. The range of values and the difference between laboratory and field data were, in part, probably due to some inadequacy in the apparatus. We have seen the cages used by Mosauer, and we believe that the temperature gradient of the experimental chamber was too steep, whereas in the field the very high temperature of 43° C. may have been due to pursuit of the lizard, to some other delay in capturing it, or to any one of a number of difficulties inherent in thermal work in the field. Errors may also result from vagaries in the reactions of the lizards themselves. However, we are inclined to accept Herter's statements that the "V.T." of lizards corresponds roughly to the climate of the habitat,

even though the temperature preference of *Agama stellio* seems open to question.

Klauber (1939) has assembled extensive data on the relationship between night collecting returns and temperature, but most of his data are confined to nocturnal ophidian species commonly found on paved highways. Although the data are those for air conditions, he emphasized the importance of the unrecorded ground temperatures. From Klauber's extensive observations made during night collecting trips, it appears probable that all our local desert reptiles ordinarily abstain from surface activity at temperatures below 60° F. (15.5° C.). Judging by their more frequent appearance during cold nights, *Crotalus cerastes* and *Rhinocheilus* seem to be more tolerant of cold than other nocturnal reptiles.

Air temperatures producing the best results for night collecting lie between 80°–89° F. (26.6°–31.65° C.). In this connection Cole (1943) has shown that a lizard's temperature is virtually unaffected by that of the surrounding air. The rate of increase in the lizard's temperature is not correlated with the ability to withstand high temperatures in any case, even though in a dry atmosphere the evaporation of moisture from the lungs is effective in cooling the animals. But desert reptiles cannot afford to use water for thermoregulation except under emergency conditions, and normally lizards neither lose nor acquire any appreciable amount of heat from the air. Cole concludes that, in the absence of sources of radiant energy, the substratum is the most important temperature determining factor.

It may be assumed that ophidians are similar to lizards in this respect but that the more extensive and intimate contact of the snake's body with the terrain should accentuate the influence of the substratum. Whereas this situation might be expected to minimize the value of Klauber's air temperature records, the micrometeorological charts of Mosauer (1936) indicate that night air temperatures are higher than those of the soil, although they are only slightly higher. However, studies, not yet complete, of pavement versus soil temperatures indicate that until midnight pavement temperatures frequently are somewhat higher than those of

the adjacent sand. The difference is slight, but it should be more than sufficient to offset the difference between the temperatures of the air and the soil. Under the conditions of Klauber's technique, it is probable that body temperatures of snakes coincide very closely with the air temperatures reported by him.

Other sources of indirect evidence bearing on the relation of temperature to reptilian activity are to be found in Klauber's (1939) reports on seasonal variation of ophidian frequency as established by the night collecting technique. May 20 to June 10 is the period showing the greatest frequency, the exact dates being subject to variations resulting from seasonal differences and altitude. From late June until the following spring, reptiles are exceedingly scarce, although there is apparently a slight resurgence of activity in late August, September, and early October. The increase in activity in autumn is notable for the preponderance of young at that time. Klauber attributes this increase to sheer numbers of the callow young and their lack of caution.

Although Klauber considers temperature to be one of the factors determining seasonal abundance, he believes that it is by no means the only one. Attempts to correlate activity with such factors as wind velocities, relative humidity, and the presence or absence of bright moonlight have been unsuccessful, but he believes that wind and humidity may be involved to a slight extent. It is inferred that the mating instinct and a post-hibernation hunt for food may furnish the stimulus leading to wandering, and that very high or very low temperatures may furnish the most important discouraging influence. Above 90° F. (32.2° C.) and below 60° F. (15.5° C.) there is a very marked regression in numbers which he believes indicated a purely thermal inhibitory effect.

There are only three truly nocturnal lizards in our desert regions, *Phyllodactylus t. tuberculosus*, *Coleonyx variegatus*, and *Xantusia vigilis*. Of these Klauber reports that only *Coleonyx* is sufficiently peripatetic to afford good night collecting. They appear to be active at temperatures as low as 62° F. (16.65° C.) and as high as 92° F. (33.3° C.) with a preference for 80°–84° F. (26.5°–28.85° C.). This conforms to the requirements

expressed for snakes, and it should be noted in connection with Mosauer's statement (1936) that there is virtually no difference between the thermal toleration of diurnal or nocturnal snakes and lizards. Nocturnal snakes and this lizard notably avoid temperatures above 33.3° C., there being only one record for *Coleonyx* at this temperature.

In a preliminary report Cowles (1942), using data from observations on eight species of diurnal lizards and six species of snakes, both nocturnal and crepuscular, states that auto-selected body temperatures of diurnal lizards are approximately 37° C., whereas those of the snakes were approximately 31° C. Furthermore he states that the snakes ordinarily avoid temperatures below 20° C. and above 33° C., and that diurnal lizards avoid those above 40° C. and below 27.4° C. From these approximations it will be seen that there is a general similarity between the findings of Cowles and those of Klauber regarding nocturnal reptiles. The differences may possibly be due to the use of body temperatures by Cowles, and of air temperature by Klauber.

It is inevitable that any discussion of thermal adaptations of reptiles should lead to a discussion of the relationship between the theories of concealing coloration, metachromatism, and the utilization and economy of heat derived directly or indirectly from sunshine. Klauber (1939), following the presentation of very extensive observations on the thermal relationships, habits, behavior, and a review of the pertinent literature, comes to the conclusion that the primary function of color is for concealment purposes rather than as a thermoregulatory device. However, he recognizes temperature regulation as an important function of color.

Atsatt (1939), following an extensive analysis of reptilian color changes in response to light and heat, states that "The color changes in the iguanids in response to temperature seem to have a thermoregulatory function. A dark lizard in sunshine obtains more warmth from the light as well as from the air: *P. platyrhinos*, taken from 17° C. and placed in sunshine for half an hour, reached a temperature of 23°–25° C. although the air temperature was only 19°–23.5° C. The change to light phase at high temperature prevents this extra absorption of heat. But what is the

value of the light phase when the lizard is in darkness at moderate temperature? If at that time the function of the light phase is to conserve heat, since a light body loses heat to a cooler atmosphere more slowly than a dark body does, why do *Crotaphytus*, *Sauromalus*, *Phrynosoma*, and *Anolis* develop this ability and yet *Dipsosaurus*, *Callisaurus*, and *Uta* with the same fundamental habits lack it?"

These and other questions raised by the phenomenon may be at least partially explained by the fact that air temperatures have little influence on either addition or loss of heat, that it is chiefly through direct contact with the substratum or through exposure to radiant energy that lizards change temperature. Cole (*supra cit.*) would agree to this emphasis on physiological function, since he concludes that the importance of protective coloration has been overemphasized. He would stress its physiological importance.

Although the reptiles with which Lueth (1941) dealt were not desert species, his observation that they may lower their temperature by means of water evaporation during respiration is in accord with the experience of Cole (*supra cit.*) and Cowles (1942). The latter writer reports observations indicating that desert reptiles may exercise respiratory or other physiological lowering of temperatures from 2° C. to as much as 10° C. under exceptional circumstances. Few experiments appear to have been conducted with aquatic reptiles whose normal environments would permit little if any cooling from evaporation. In this connection Baldwin's report (1925) is of possible significance. He reports that two species of fresh-water turtles (*Chrysemys* and *Chelydra*) showed signs of discomfort at 80° F. (26.5° C.). Increasing environmental temperatures were accompanied by corresponding rises in body temperatures and, "as a

rule," these were fatal if maintained at 102° to 105° F. (approximately 39° to 40.5° C.) for 30 minutes or more.

Cowles (1941) has mentioned another factor which is involved in the adaptation of reptiles to desert climates, namely, size. In this account, the advantages accruing to lizards of small size are described. The smaller species, or the young of the larger animals, are capable of more rapid heating in sunshine than are the large lizards. An additional advantage in small size is the utilization of smaller particles of food which, because of the more favorable surface-mass ratio, should expedite digestion.

An evident disadvantage inherent in smallness is the greater susceptibility to overheating during the summer months when this constitutes the greatest hazard. Cole (*supra cit.*) objects to this suggestion on the basis of his observations on temperature responses, some of which he made without using radiant heat as an energy source. This is an important consideration because the lizards referred to are diurnal forms living in desert climates, and their chief hazard comes from the potency of the sunshine when they are out in the open where they must frequently go to seek their food. When these animals retreat to underground shelters, where ample cooling is available in the substratum, their body heat is dissipated very rapidly. Cole was inclined to lay greater emphasis on the fact that small body size permits rapid cooling.

Some of the evolutionary implications which seem to be inherent in the thermal sensitivity and dependence of reptiles have been discussed at some length by Cowles (1939, 1940, and 1944). In these papers the possible importance of temperature in the evolution of terrestrial vertebrates has been stressed.

MATERIALS AND METHODS

REGION AND TERRAIN

THE REGION WHEREIN most of these experiments were conducted presents typical aspects of the Coloradan subdivision of the Lower Sonoran life zone. Cages and other equipment were installed in the field, as described hereinafter, at a locality near Indian Wells, Riverside County, California. This locality lies on the floor of the Coachella Valley a few feet above sea level, with drainage to the southeast into the sink of the Salton Sea. The surface of this body of water is below sea level.

Coachella Valley is flanked on the northeast by the Little San Bernardino Mountains, and on the southwest by the Santa Rosa and San Jacinto Mountains which rise to a maximum elevation of 10,805 feet (pl. 19) on the highest peak (Mount San Jacinto). Within a radius of a few miles, therefore, it was possible to obtain diverse species of reptiles, including arenicolous and subterranean forms inhabiting the floor of the valley, and rock-dwelling forms in the foothills and canyons of the adjacent mountains. Farther up the mountain in associations referable to the Upper Sonoran zone many other species occur that are characteristic of the cooler, more humid coastal climate of southern California. Most of the animals used in our experiments were secured in the vicinity of Indian Wells. For comparative purposes, however, we have utilized data derived from specimens taken in the Yuma sand dunes and others secured on the Mojave Desert to the north at somewhat higher elevations. In one instance the data presented were drawn from observations made in the field on *Crotaphytus silus*, a lizard endemic to southern San Joaquin Valley.

Coachella Valley itself is a region of exerophytic vegetation. It is a desert of extreme heat and aridity, characterized by sporadically abundant annual, and scanty perennial, vegetation (pl. 20, figs. 1, 2), the latter usually growing to a height of only a few feet at most. A few plants of more robust growth, for instance the desert willow, *Chilopsis linearis*, palo verde, *Cercidium floridum*, the smoke-tree, *Dalea spinosa*, and the ocotillo, *Fouquieria splendens*, may be fairly abundant

locally, but individual plants are scattered. The only concentrations or groves of native trees consist of thicket-like growths of the mesquite, *Prosopis chilensis*. Although these thickets may become fairly extensive, ranging in size from a few to several hundred meters in length and breadth, they are usually small and confined to a few areas where the water table is sufficiently shallow to allow their roots to reach the adjacent moist soil.

Since the untempered heat of desert areas is fatal to all native reptiles, it is important to recognize the fact that shade, and thus vegetation, is an essential item in the habitat of most species of these animals. Except for a few weeks in spring, extensive and relatively unbroken shelter is available only in the mesquite thickets, with rather specialized ecological conditions (pl. 21, fig. 1), or under some of the numerous small and compact but abundant plants such as burrowweed, *Franseria dumosa*, cheese-bush, *Hymenoclea salsola*, and white-ratany, *Krameria Grayi*. Over most of the desert, sparse shade may be found in the vicinity of the dominant creosote-bush, *Larrea divaricata* (pl. 21, fig. 2).

The most notable characteristics of the desert habitat are the omnipresent burrows, crevices, and holes (pl. 22, figs. 1, 2), into which reptiles can retreat without moving more than a few yards, and the almost universal presence of loose sand or gravel which facilitate burrowing.

For a few weeks each spring, the ephemeral annual plants (pl. 20, fig. 2) provide abundant shade, but their chief value seems to lie in the forage that they provide for the insects on which most lizards feed. To a limited extent these plants are of direct value to a few herbivorous lizards, and they are a source of occasional dietary additions to the menu of the many insectivorous species, including *Dipsosaurus*, *Sceloporus m. magister*, and possibly *Crotaphytus collaris baileyi*.

Summer temperatures are high, sometimes rising to 55° C. (or to as much as 130° F.). During many of the winter nights freezing temperatures are not uncommon, although the days are usually mild. A diurnal-noctur-

nal temperature range of as much as 30° C. is not infrequent. During the spring of 1938 temperatures taken at the ground surface ranged from 5° C., even as late as April, to a

maximum, recorded in full sun on a black-bulb thermometer, of 87° C. during the last week of May. The highest shade temperature during May was 45° C. (113° F.).

EXPERIMENTAL PROCEDURE

In order to maintain an environment as nearly as possible like that which the animals would occupy in nature, wire netting cages (pl. 23, fig. 1) were constructed in a large clearing in a thicket of mesquite trees.

Shade was provided by 45-mm. squares of "Cellotex," 20 mm. in thickness, placed 250 mm. from the ground. Even under these well-insulated shelters, reflected heat influenced the temperature by as much as 5°–6° C. Additional shelters, for use when shade temperatures became insupportable above ground, were available in the form of iron pipes 100 mm. in diameter, buried in the ground in such a manner as to place the lowest end 450 to 500 mm. below the surface. The insides of these pipes were rough enough to provide traction surfaces for snakes and lizards. The non-jumping lizards were usually confined in a circular enclosure of smooth galvanized iron thrust 100 mm. into the ground (pl. 23, fig. 2).

As already noted, it was found that the behavior of reptiles in confinement was likely to be more normal in the presence of an observer than that of free animals. In so far as possible, data were recorded only when stimuli and responses fitted an apparently normal pattern. As the surrounding temperatures rose or fell, the animals were kept under close observation until each new response to thermal stimuli was observed. The lizards were then noosed and their temperatures were taken by means of a carefully calibrated thermocouple.

At the start of these investigations both deep esophageal and cloacal temperatures were taken, but it was found that the former were invariably lower than the latter. Consequently esophageal records were discarded as representing a doubtful approximation of the actual body temperature, and only cloacal temperatures were utilized.

The presence of consistently lower temperatures in proximity to the moist surfaces of the respiratory tract is indicative of considerable heat dissipation resulting from

evaporation. We infer that the condition furnished indirect evidence of the nature of thermal regulation reported elsewhere in this paper. From 26 readings it was determined that the cloacal temperatures of the snake were 3° C., and those of the lizards 2.8° C., above those taken in the esophageal region. Under any circumstances the tight clamping of the jaws in lizards makes the taking of routine buccal temperatures quite impractical. The inevitable delay and the alternative necessity of violently forcing the mouth open make the procedure undesirable.

Although gloves were not employed in the earlier stages of these experiments, it has been found advisable to interpose some insulating substance between the operator's hands and the animal's body. The procedure is imperative whenever there is a great temperature difference between the two.

One of the most notable characteristics of these animals is the rapidity with which they absorb or lose heat. A small lizard may gain 2°–3° C. while being held in the hand waiting for the thermometric instruments to reach equilibrium, and even a lizard as large as an adult *Sceloporus m. magister* will absorb heat so rapidly that the temperature will rise 0.5°–1° C. per minute. This factor appears to have been overlooked in some experimentation. Even under the most favorable circumstances and with the best of instruments, there are such rapid changes in the body temperatures of very small reptiles that the instrumental lag produces results with an accuracy no better than $\pm 1^\circ$ C. The rapid changes in reptilian temperatures seem to be due primarily to: (1) their lack of effective surface insulation; (2) lack of hypodermal adipose tissue; (3) their pigmentation, particularly the melanin; and (4) in the smaller species, to the relatively small volume with a proportionately large temperature-conducting surface area.

As will be noted throughout this paper, reference is made to several types of thermo-

metric records, and these require some explanation. The black-bulb thermometer was of the usual type, a regulation mercury thermometer with the bulb carbon-blackened and hermetically sealed in a glass test-tube. It was adopted in order to measure temperatures by a device that would give more nearly representative indications of maximum heat conditions found in direct sunlight

sunlight at a point barely below a thin covering of sand, and recorded at an approximate depth of 2 mm. The thin surface film of soil was necessary in order to eliminate the effect of direct sunlight striking the thermometer bulb. Although this method does not give the absolute maximum temperature of the surface film, it was the only practical procedure available. Because the movement of an ani-

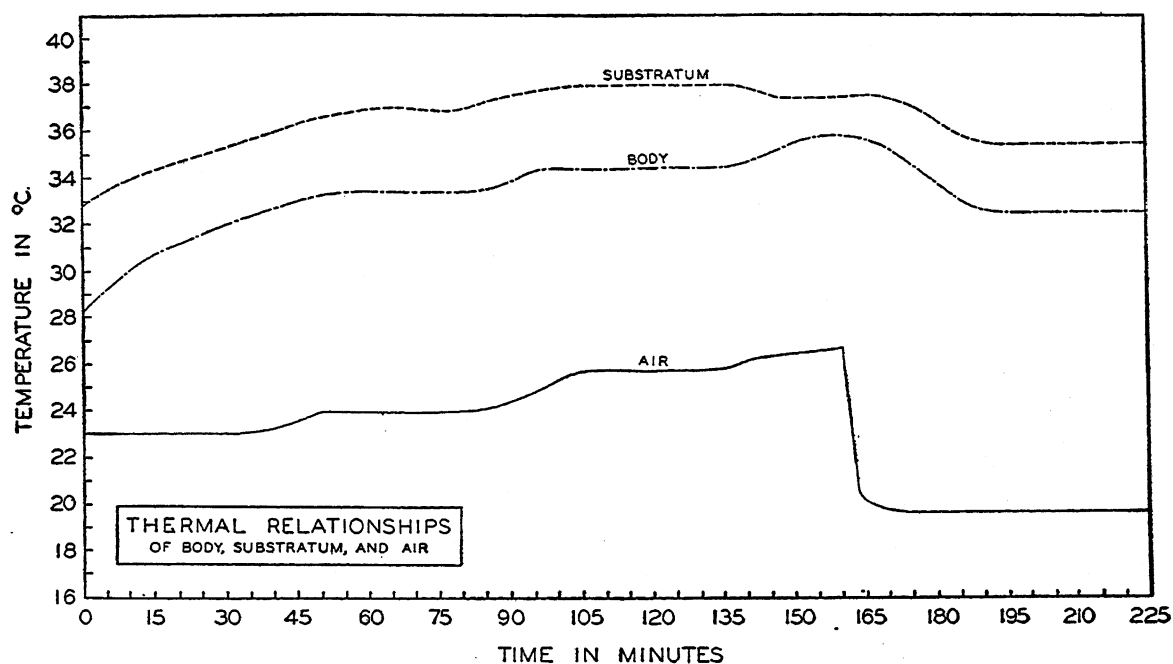


FIG. 1. Thermal relationships of body, substratum, and air, as observed in an experiment with an adult male *Sceloporus m. magister*. The experimental animal was held in place on a slab of slate 4 mm. thick, with a conductivity index of 0.0045, and temperatures were recorded with a thermocouple at five-minute intervals over a period of three hours and forty-five minutes. The slate was heated from below with a thermostatically controlled heating element when the air temperature was near the minimum voluntarily tolerated.

than are obtainable by the use of clear glass bulbs. It was found that the heat absorption capacity of this instrument is more nearly like that of a dark-bodied lizard than is the standard, unblackened thermometer. The similarity between the heat absorption of a lizard and the black-bulb thermometer is reported later in connection with the side-blotched lizard, *Uta stansburiana stejnegeri*. However, the changing albedo of lizards prevents the development of a fully satisfactory thermometer.

Surface temperatures were obtained in full

mal frequently displaces as much or more of the surface layers, the temperatures taken in this manner should be satisfactory.

Shade temperatures were obtained from freely circulating air, in a palm-leaf shelter 3 feet above the ground. The site provided records which are approximately the same as those obtainable from a standard weather-bureau shelter. These data were accumulated both for comparison with weather reports on temperatures and for use in determining the actual thermal difference which exists between temperatures observed under conven-

tional conditions and those which exist at levels near the ground where lizards are more commonly found.

Experiments conducted for the purpose of determining the relative importance of air

thick was selected. This material has a conductivity index of 0.0045, as compared with 0.0047 for granite, 0.0055 for sandstone, 0.0033 for dry sand. Reference to the graphs in figures 1 and 2 provides a satisfactory in-

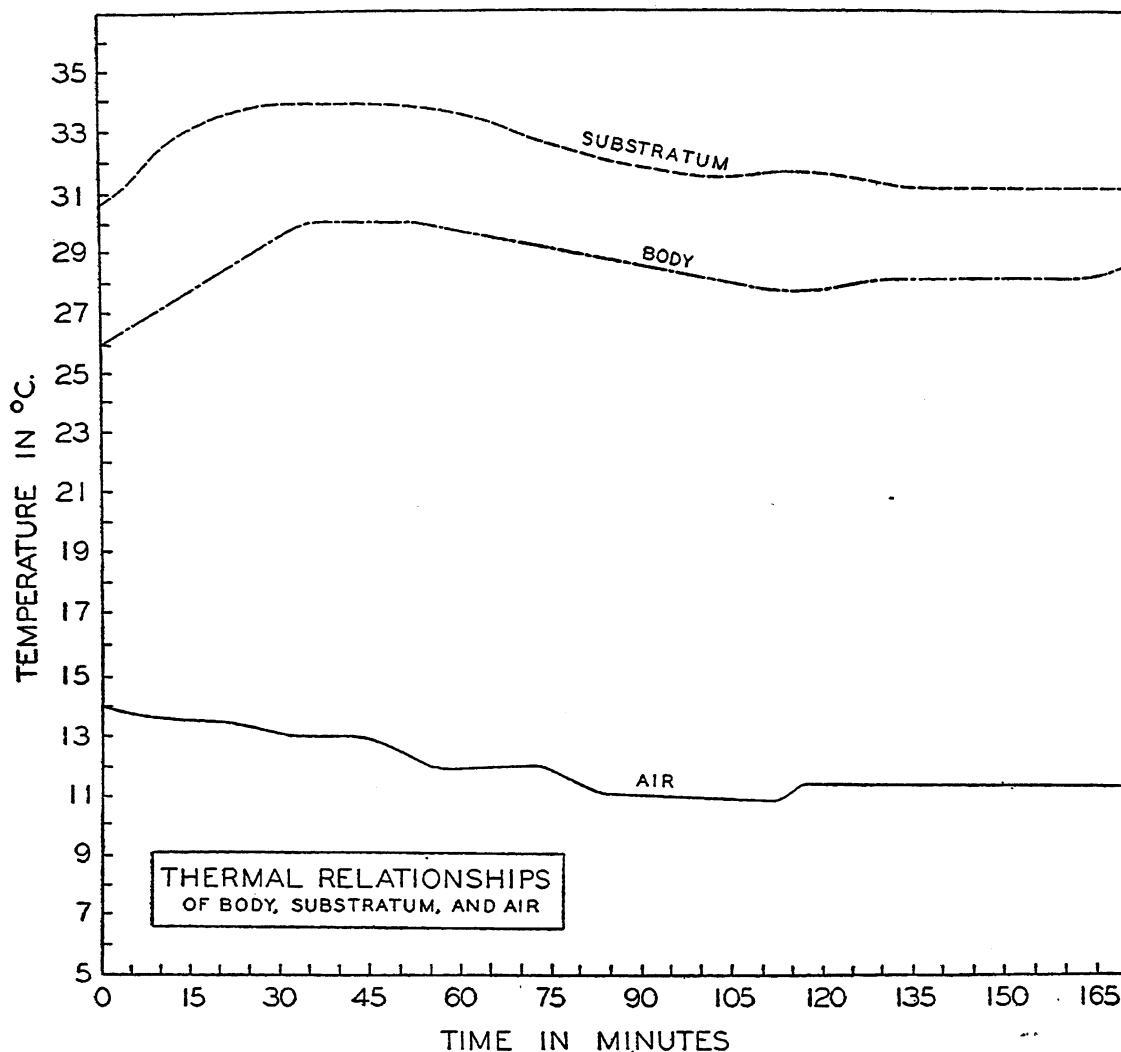


FIG. 2. The experimental conditions were the same as described in the caption for figure 1, except that thermocouple readings were recorded at five-minute intervals for two hours and fifty minutes when the air temperature was below that ordinarily tolerated.

temperatures versus those of the substratum have shown that the diversity in conductivity and texture of rocks, sand, dirt, and dust is so great as to preclude an exact measure of their respective efficiency in transferring heat. As a compromise substance, a slab of slate 4 mm.

dication of the relationship between temperatures of the substratum at the point of contact with the body, and those of the body and air, under conditions of varying temperatures of air and substratum.

The experimental animal used to obtain

data for these graphs was a lizard, an adult male *Sceloporus m. magister*, held in place by tabs of transparent cellulose adhesive tape. All temperatures were recorded by means of a thermocouple. The temperature ranges are within the limits which might be expected under natural conditions.

For the reasons set forth above, it has been

found necessary to discard about 80 per cent of the data that had been accumulated for this discussion of the thermal relationships of reptiles. It is believed that the resulting rigorous pruning has left a residuum of information that should be of help as an outline and indicator of some of the interesting and significant aspects of reptilian ecology.

CRITERIA USED IN RECORDING TEMPERATURES

Following some preliminary observations it became apparent that ecologically important thermal reactions of desert reptiles could be divided into the following general major categories:

1. **THE LETHAL MINIMUM:** This may be described as the low temperature that will cause death from short exposures where the factor of exhaustion does not influence the outcome.

2. **THE CRITICAL MINIMUM:** From the ecological standpoint this is equivalent to the lethal under certain conditions, since it is the temperature that causes a cold narcosis and effectually prevents locomotion. At this temperature the animals are helpless to escape enemies or to remedy their thermal impasse if they have not already sought sanctuary.

3. **THE VOLUNTARY MINIMUM:** The low temperature that will cause diurnal animals to become photophobic, or to retreat to their underground shelters; or in the case of nocturnal animals it is the temperature that will drive them underground even though this may lead them to still lower temperatures.

4. **THE BASKING RANGE:** This is a difficult category to delimit either by observation or by experiment, because it is not sharply set off from the next higher stage. It extends to the thermal point at which the desire for basking yields to the stimuli that lead to ordinary routine activity.

5. **NORMAL ACTIVITY RANGE:** This is the thermal range extending from the resumption of ordinary routine (after the animal has ceased basking, in the case of diurnal forms) and terminates at a point just below the level at which high temperatures drive the animal to shelter. The entire range, stated as the mean in this account, may be considered as an ecological optimum as distinguished from the physiological concept of the most favor-

able temperature as a distinct entity. Defecation is closely associated with the attainment of normal operating temperatures, and it may signify a resumption of active peristalsis.¹

6. **MAXIMUM VOLUNTARY TOLERANCE:** 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.

7. **THE CRITICAL MAXIMUM:** This appropriately can be termed the potential lethal and may be defined as the thermal point at which locomotory activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death. Recovery from this incapacitation is the criterion for determining whether or not the animal has been exposed to unnecessarily high temperatures. From the ecological viewpoint it is the lethal temperature.

8. **THE LETHAL:** The high temperature that produces irreversible and fatal bodily damage. Because body temperatures rise rapidly when the effectiveness of respiration is seriously impaired, and since signs of life remain even after fatal damage has been incurred, it is exceedingly difficult to determine the exact thermal point responsible for death. In addition to this difficulty, a somewhat lower temperature may cause death if the exposure is sufficiently prolonged.

The reversibility of the phototropic response at the above-noted thermal levels is an interesting protective device. It is noteworthy that supranormal temperatures, those just below the lethal level, frequently induce an additional reversal of behavior so that when over-heated lizards are afforded their choice of either light or dark areas, they emerge into the light. Often they will dash

¹ For this observation we are indebted to Mr. S. D. Hinton, a former student of the senior author.

toward the brightest point, presumably responding as they would to the brightly lighted exit from an underground retreat.

Although these are the more obvious divisions of thermal responses, there are probably other and more subtle distinctions that can be ascertained only by other experimentation. It is entirely possible, for instance, that these animals may partially emerge into the open to bask before their neural and muscular requirements have reached a thermal point where the maximum celerity of their responses is sufficient to protect them from the danger of predation. (In this connection, see the discussion under *Sauromalus* hereinafter.) Under these conditions they remain within a few inches of the home retreat. There are few herpetologists who would deny that lizards are more easily approached and captured during the cooler hours of the day than they are during the hot midday period when their temperatures are at the highest tolerable level. Many desert lizards, of course, retreat during the hours of most intense heat, as Klauber (1939, p. 69) notes.

Virtually nothing is known about the thermal requirements for normal digestion, such as the velocity of action by the enzymes at different temperatures, peristaltic stimulation, and the like. Yet in the diurnal desert reptiles defecation seems to require certain temperatures, apparently between 32° and 37° C. Among other examples of subtle and not readily perceived thermal effects is the fact that the males of the yucca night-lizard (*Xantusia vigilis*) are sterilized by temperatures which seem to cause no discomfort and which they can survive for at least a week or more (Cowles and Burleson, 1944). If this condition is widespread among reptiles, its significance can scarcely be overestimated.

Of the eight thermal levels that have been described, the first two were found unsuitable for field study and they have been relegated to laboratory experimentation. Of the rest, all

but the lethal temperature were found to be satisfactory for field and cage study.

In obtaining data for the critical maximum or potential lethal temperature, the experimental animals were either liberated in an enclosure from which all shade and shelter had been removed, or they were tethered so as to provide freedom of movement while preventing escape. Shade was always visible within a short distance, and the animals were allowed to struggle toward this objective until effective coordinated movements had ceased. At this point they were removed to shade in order to prevent any appreciable additional heat absorption, and their temperatures were measured as expeditiously as possible. Data derived in this manner were considered valid only if the experimental animals subsequently recovered. Thus the effects of temperature rise following impairment of respiration are reduced to a minimum in our records.

The taking of the lethal temperatures followed much the same general procedure, except that heat collapse was allowed to progress until the animal relaxed. Very few lethal temperatures were obtained, as it was felt that the sharp rise in temperature attendant on the primary collapse obscured the temperature that was actually responsible for death.

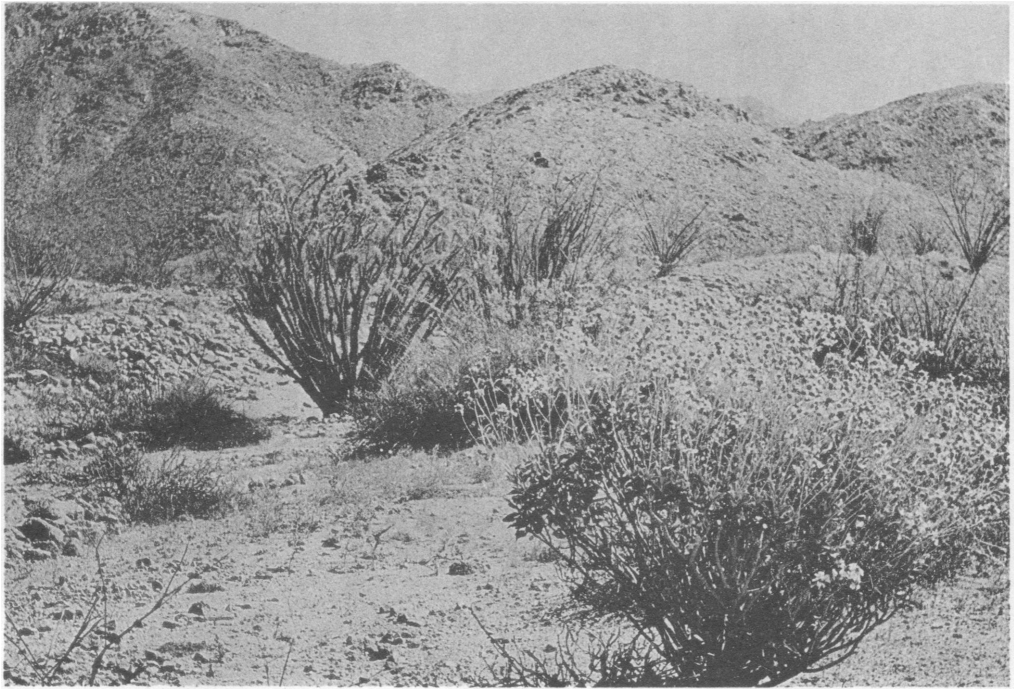
With practice, an increasing familiarity with the animal's normal behavior allowed an experienced observer virtually to predict reactions a few seconds before they took place, and there ensued a corresponding diminution in the number of rejected data.

The small amount of field data included in this report can be ascribed to the rather drastic rejection of notations due to such temperature distorting factors as a prolonged chase prior to capture of the lizard, temporary escape into the shade or sunlight, and particularly to the fact that it is exceedingly difficult to know the essential facts concerning antecedent activities.

PLATES 19–29



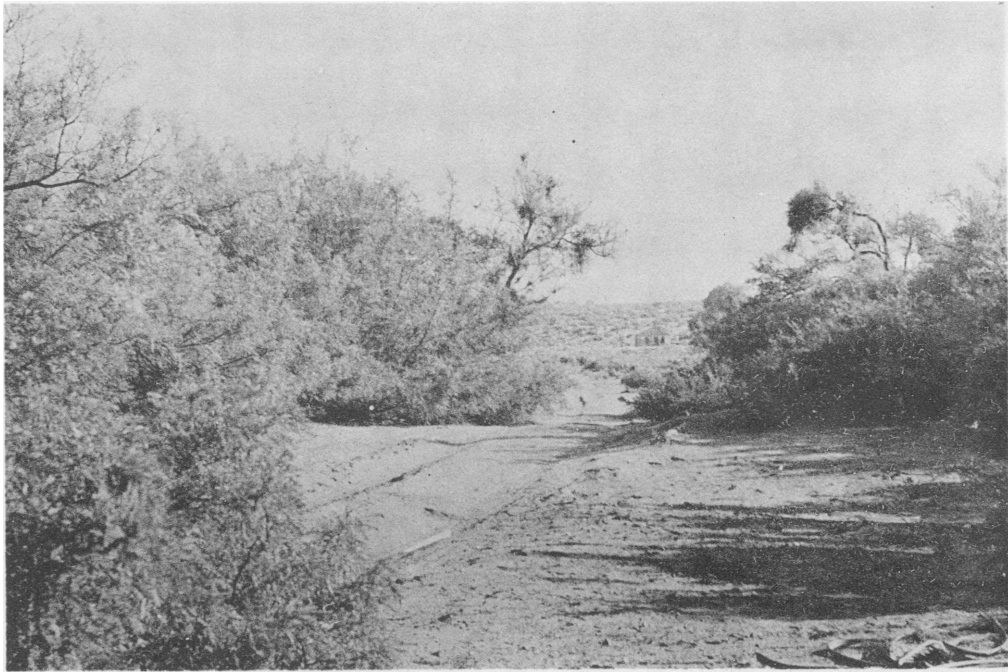
Air view of the northeastern escarpment of Mount San Jacinto in Riverside County, California. The town of Palm Springs lies at the foot of the mountain at an elevation of scarcely 500 feet. The summit of San Jacinto Peak, 10,805 feet above sea level, is within an air-line distance of 3 miles from the foot of the mountain. Such reptiles as the desert horned lizard (*Phrynosoma p. platyrhinos*), the sand lizard (*Uma inornata*), the desert iguana (*Dipsosaurus d. dorsalis*), the glossy snake (*Arizona elegans occidentalis*), the leaf-nosed snake (*Phyllorhynchus d. perkinsi*), the shovel-nosed snake (*Chionactis o. occipitalis*), and the sidewinder (*Crotalus cerastes*) in this particular region are more or less restricted to the Lower Sonoran sandy flats at the foot of the mountain. The chuckawalla (*Sauromalus obesus*), the collared lizard (*Crotaphytus collaris*), and the giant uta (*Uta mearnsi*) inhabit the Lower Sonoran rocky foothills. Reptiles occurring in the Transition and Boreal zones near the summit of the mountains include the rubber boa (*Charina bottae umbratica*), the Pacific rattlesnake (*Crotalus viridis oreganus*) and the western skink (*Eumeces s. skiltonianus*). Some of the Lower Sonoran reptiles are restricted to either sandy or to rocky habitats. (Photograph courtesy of Lt. Frank Bogert.)



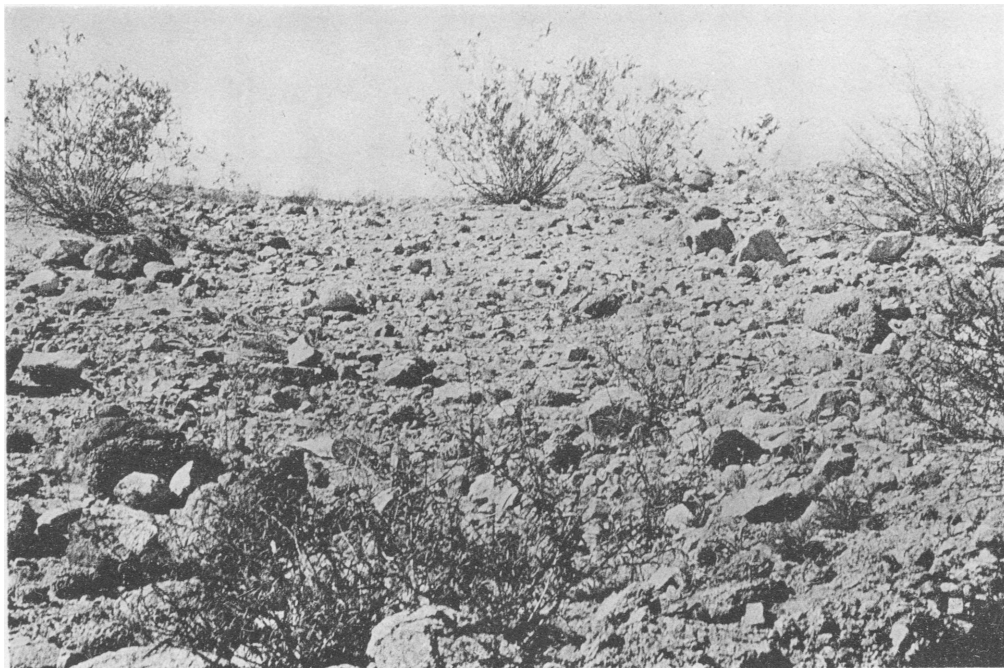
1. Scanty perennial vegetation in deserts provides limited and interrupted shade. Right foreground, *Encelia farinosa*. Stems of the ocotillo, *Fouquieria splendens*, show against background of hills



2. Annual vegetation of many species provides only an ephemeral source of shade



1. Dense and continuous shade is provided in limited areas by the mesquite, *Prosopis chilensis*. The specialized conditions in these thickets permit their occupation by only a few species of reptiles, the most common being the desert diamondback rattlesnake, *Crotalus atrox*



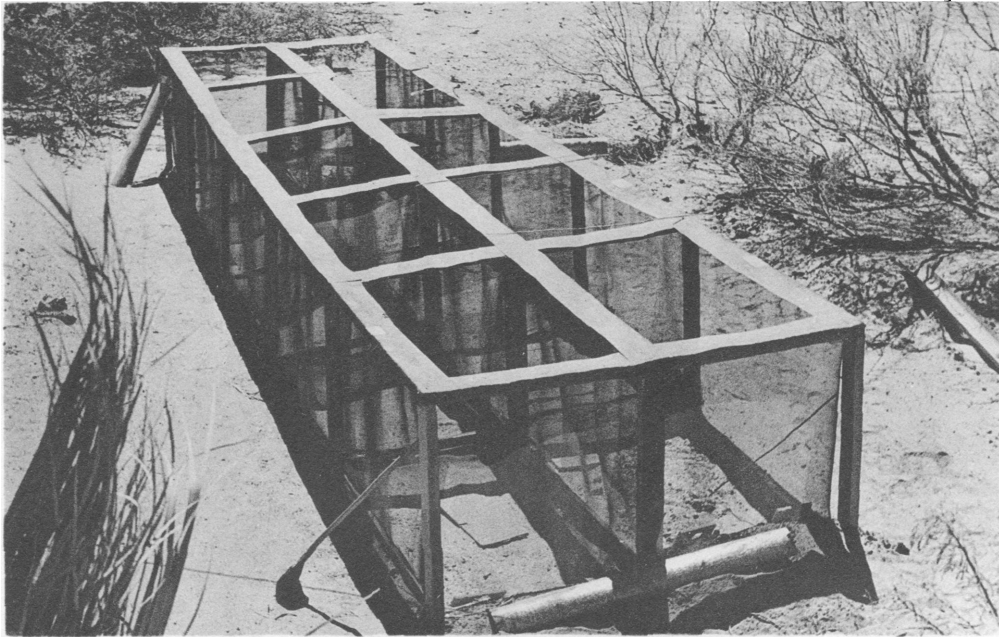
2. Typical sample of a rocky desert where scanty shade is provided by the creosote bush, *Larrea divaricata* (against skyline), and by the thickly strewn boulders. Only the smaller lizards find accommodation in such an area



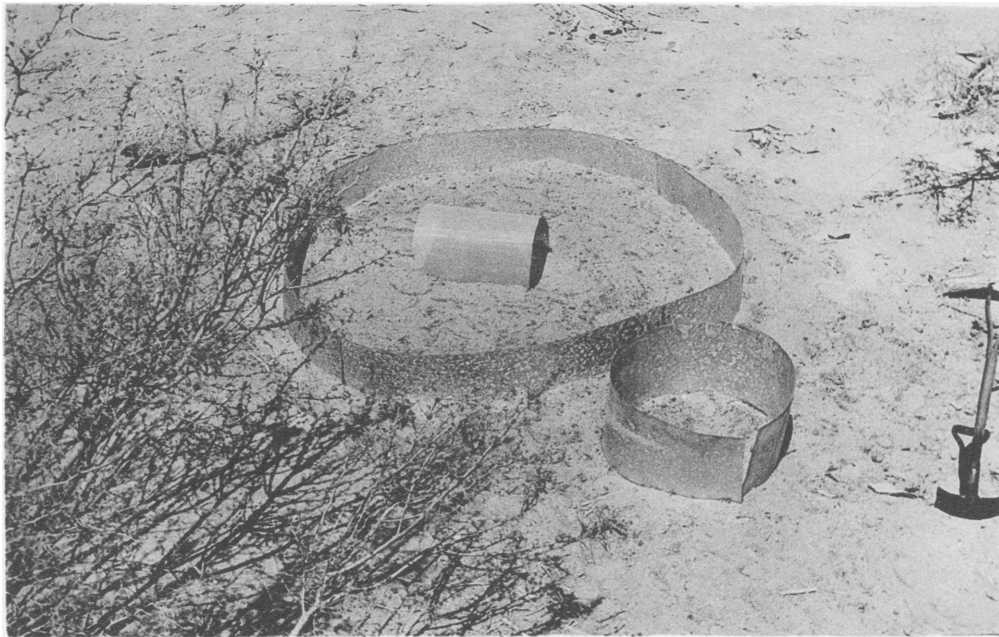
1. The densely perforated banks of most washes furnish many species of reptiles with readily accessible shelter



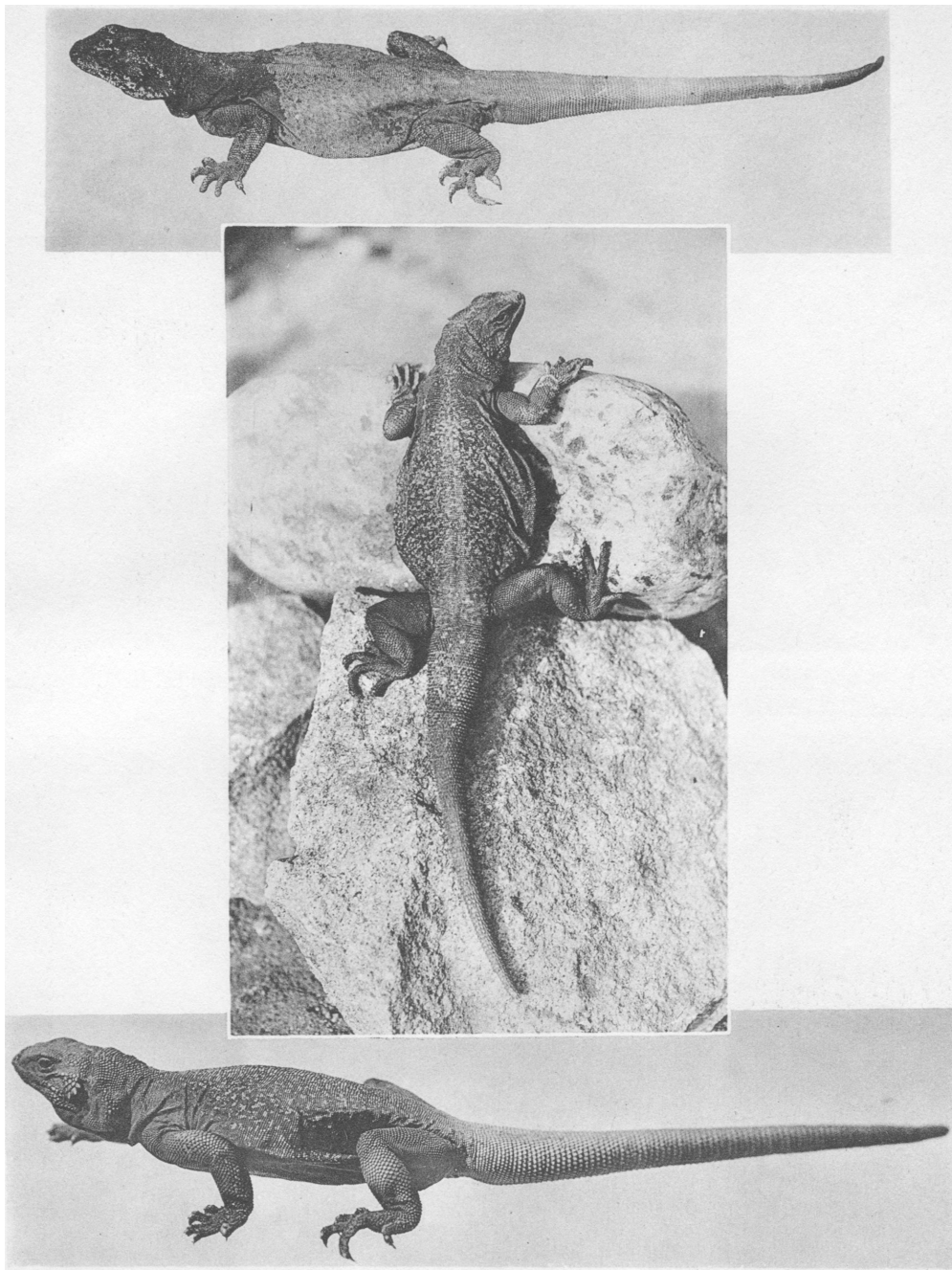
2. The ground beneath perennial desert plants is often honeycombed by an extensive network of interconnecting tunnels that provide abundant shelter for many species of desert reptiles



1. Wire-netting cages set up in the field and used to maintain reptiles under observation. Note the overhanging strips on top to prevent the escape of experimental animals



2. Galvanized iron collars used to confine small reptiles such as the horned lizards which are unable to jump



Chuckawallas (*Sauromalus obesus*). 1. Adult male from Colorado Desert. The pattern is characteristic of a local population in the Orocopia Mountains, Riverside County, California. 2, 3. Adult male, dorsal and lateral views, with darker pattern characteristic of most populations in the Mojave Desert. Specimen from Lovejoy Springs, Los Angeles County, California



1. Slowly decomposing logs of the Joshua tree, *Yucca brevifolia*, the typical habitat of the night lizard, *Xantusia vigilis*



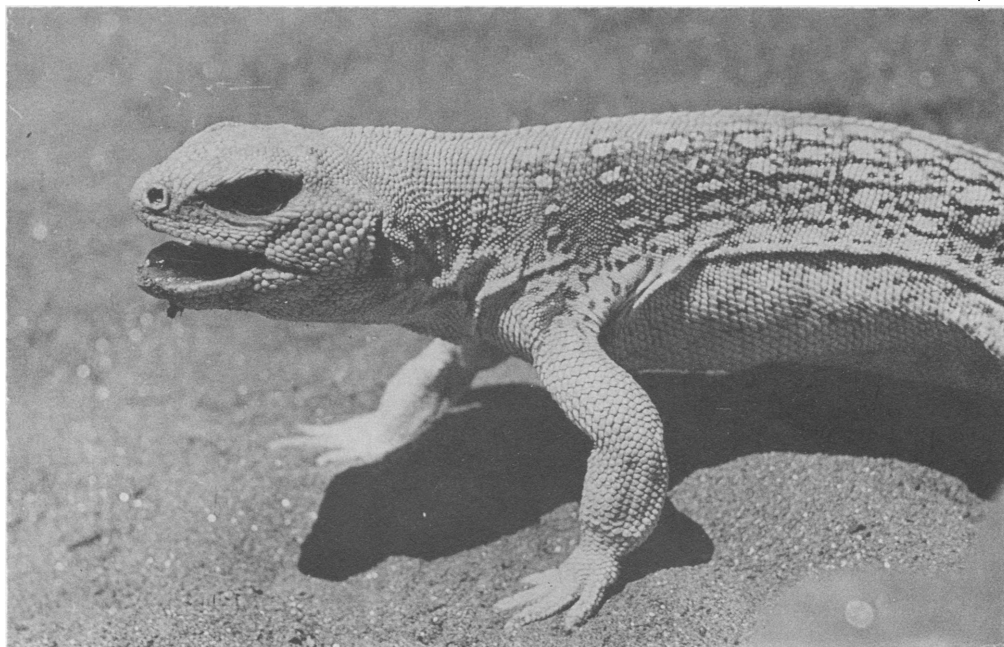
2. Snow-covered Spanish bayonet, *Yucca whipplei*, at extreme western limits of the range of *Xantusia vigilis*



1. Sidewinder, *Crotalus cerastes*, exposed to sun at 10 A.M., July 15. The snake is lying flush with surface of sand in a self-made depression. Photographed on the Colorado Desert



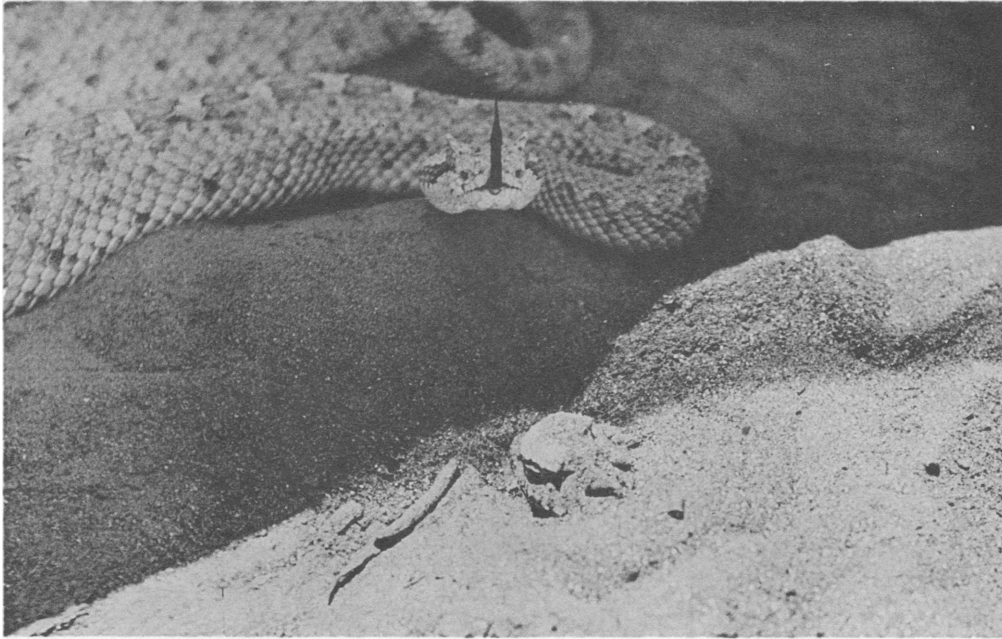
2. Depression in sand excavated by *Crotalus cerastes*, September 15. The bedding-down place had been vacated prior to its discovery about 11 A.M. Illustration shows tracks made on entering and leaving the site



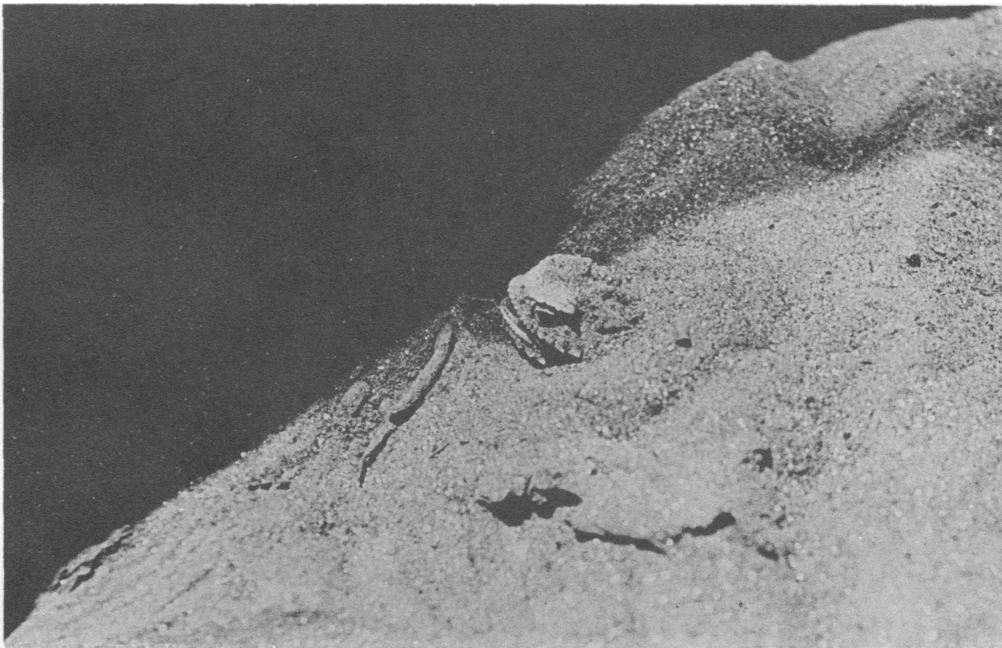
1. Desert iguana, *Dipsosaurus dorsalis dorsalis*, under conditions of excessively high temperature. The open mouth and strongly compressed abdomen are illustrative of the exaggerated respiration adopted during exposure to great heat



2. Western glossy snake, *Arizona elegans occidentalis*. Posture assumed after exposure to excessively high temperature. The angular bends in the body are characteristic of snakes exposed to near-lethal temperatures



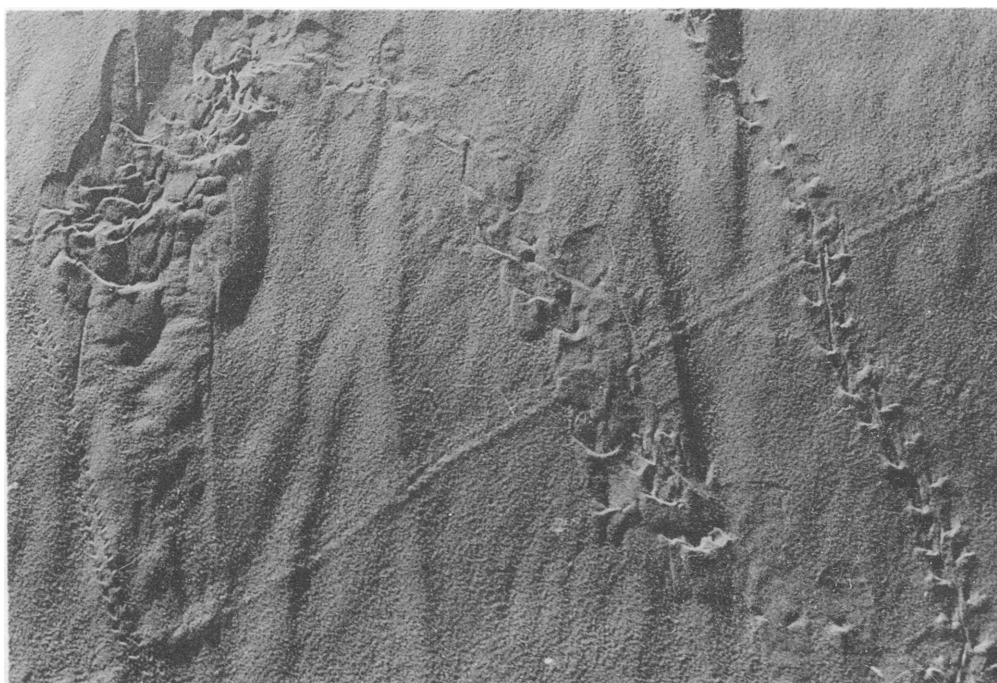
1. Sidewinder, *Crotalus cerastes*, monopolizing shade while a desert horned lizard, *Phrynosoma p. platyrhinos*, is compelled to remain in the hot sand at the edge of shadow



2. *Phrynosoma p. platyrhinos* under above conditions showing signs of extreme heat. Note the open mouth associated with "panting" at high temperature



1. Desert horned lizard, *Phrynosoma p. platyrhinos*, *in situ* during pre-emergence basking. The head is left center and the point of initial submergence is near the right margin. The dense shadow at the center represents point at which night was spent; movement forward and upward produced the depression behind body



2. Resting place of *Uma inornata* on the face of a sand dune, at left center. The animal departed after early morning basking. The tracks indicate leisurely procedure to the lower right, and ascent up right center. The diagonal tracks of smaller size are those of a beetle, probably *Eleodes*

EXPERIMENTAL RESULTS

LIZARDS

Coleonyx variegatus, Banded Gecko

The thermal responses of this nocturnal lizard closely approximate those of the nocturnal snakes. It is able to crawl at temperatures as low as 11° C., but in actual practice the animals do not ordinarily expose themselves to temperatures below 16° C. As a matter of fact, they are rarely found in the open below air temperatures of 18° C., except when the ground is warm.

Whereas this gecko appears to be somewhat more resistant to cold than the snakes, it is also capable of enduring somewhat higher temperatures than these animals. For the snakes as well as for this lizard, the activity range lies in the vicinity of 30° C. This is well below that of the diurnal lizards.

The small number of available specimens has prevented a satisfactory determination of the critical maximum, but this point is reached at a body temperature somewhat below 41° C. Under extreme conditions of heat and with relative humidity at 11 per cent, respiratory cooling of about 2.5° C. has been noted.

Dipsosaurus dorsalis dorsalis, Desert Iguana or Northern Crested Lizard

After one night of exposure to temperatures slightly below 8° C., a common night temperature in early spring, these lizards are torpid and often so sluggish that they are unable to move. As their body temperatures rise with increasing warmth, they remain helpless up to 14° C. At 18° C. they are unable to coordinate rapid movements, and they resort to clumsy intimidation displays. A temperature of 21° C. permits slow locomotion, and at 24° C. torpidity is still evident but the animal can walk with well-coordinated movements. The temperature of 27° C. constitutes a well-defined minimum voluntary tolerance.

It is notable that at low temperatures this species of lizard is more seriously discommoded than are some others that have wider territorial ranges. Normal activity extends from 34°–41° C., and the mean for all records (38 observations) is 37.4° C. Retreat from high temperatures observed in 20 caged ani-

mals over a period of two months indicates that they avoid exposure to body temperatures of more than 41° C. Nevertheless, lizards under apparently ideal conditions were recorded with temperatures of 42° C. immediately after they were shot, and on six occasions lizards captured alive had temperatures of 43° C. Although the lizards that were shot did not give any evidence of prolonged exposure resulting from fear of the collector, the noosed lizards assumed the usual state of tonic immobility attendant on the presence of danger. However, it did not appear probable that there had been time for any abnormal heat absorption. Until additional observations are possible, it seems advisable to consider 41° C. the maximum normal temperature tolerance.

Desert iguanas taken near Indian Wells on the Colorado Desert reach the critical maximum at 47.5° C. (6 trials; min., 47° C.; max., 48° C.). A like number from Saltdale, a locality at a higher elevation on the Mojave Desert, under experimental conditions reached the critical maximum at 47° C. Three of the animals were again subjected to the same test and at the end of 30 minutes collapsed and died at 47° C.

Only two tests for the so-called lethal temperature have been made, one based on an individual from the Mojave Desert and another from the Colorado Desert. The one from the cooler Mojave died at 50° C., the other at 50.5° C. The difference is doubtfully significant and probably not the result of climatic adaptation.

Crotaphytus wislizenii, Leopard Lizard

Only one individual was available for study. After repeated observations over a period of two weeks it became evident that this animal invariably retreated to cover when lowering temperatures approached 23° C. Other observations did not yield conclusive data.

Crotaphytus silus, Short-nosed Leopard Lizard (from southern San Joaquin Valley)

The following data were assembled in the field. Each animal was noosed and its tem-

perature measured immediately. No information obtained from a prolonged stalk, pursuit, or other delay has been included. On the basis of seven records, the activity range or optimum expressed as the mean appears to be 38.7° C.

Lizards captured in the shade registered a minimum of 37° C. and a maximum of 39.5° C. Records from basking lizards registered a minimum of 38° C. and a maximum of 41° C.

Sauromalus obesus, Chuckawalla

At 14° C. these animals are scarcely able to right themselves from a supine to normal position.¹ At 21° C. slow but effectual locomotion is possible, while at 24° C. the fear response seems to be dulled, a distinct contrast to the condition in *Dipsosaurus* where fear and alertness seem to reach the normal pitch at this temperature.

Fifteen observations were made on wild individuals obtained on the Mojave Desert in the course of a single cloudy day. Throughout the period, air temperature remained at 24° C., while the temperature in the crevices occupied by the animals was 25.5° C. Although all the individuals were discovered in rock crevices, none of the animals was more than halfway to the bottom of its retreat. Reluctance to appear in the open at what seem to be entirely tolerable conditions apparently endows these animals with an excellent safeguard against capture by predators; apparently chuckawallas do not expose themselves to view until their body temperatures have risen to the point where celerity of responses insures their ability to escape.

It was instructive to find that the lighter colored, but somewhat smaller individuals from the Colorado Desert absorbed heat more slowly than the black-and-dark-red color phases more characteristic of the cooler Mojave Desert (pl. 24). At maximum temperatures attainable under moderate thermal conditions, a large black and red individual

reached a temperature 2° C. higher than that of smaller, lighter colored individuals. In spite of its darker color and more effective heat absorption, the larger lizard required a longer time to reach its ultimate thermal level. This is consonant with the change in surface area relative to the changed mass of an organism. The influence of color on rate of absorption can be determined to an exact degree only by the use of two series of lizards of different color but having identical surface areas and mass.

Chuckawallas should furnish an excellent source of information on the importance of color as a physiological adaptation versus its value as a means of concealment. The color variability (but not metachromatism) that is found within any one species of the horned lizard (*Phrynosoma*), fringe-footed lizard (*Uma*), and many snakes seems to be a device of primary importance in concealment. The same may be found true in the chuckawalla which displays a high degree of color variability in different localities, particularly in the Colorado Desert.

The darker coloration of the Mojave Desert form may reflect a need for greater heat absorption consonant with its larger size and the cooler climate of this higher desert. The various pattern phases represented in the warmer Colorado Desert are lighter colored on the body, although the head is nearly completely black (pl. 24, fig. 1). It is pure speculation, but it seems possible that such a pattern enables these Colorado Desert lizards to absorb heat rather rapidly when only the head is protruding from a crevice. On the other hand, the yellow coloration of the trunk would not absorb heat so rapidly as would the red and black body of the Mojave Desert form when these lizards venture forth into direct sunlight. Such a black and yellow pattern, therefore, may represent an evolutionary compromise. On the other hand, such a pattern can be interpreted as disruptive coloration. Klauber (1939) has pointed out that black rock or the dark areas resulting from shadows in a paler rock habitat may make it difficult to distinguish the body outline of these dusky colored lizards. Hence their coloration may be of protective value. It is noteworthy, however, that large diurnal lizards in all parts of the world tend to be

¹One of the most peculiar reactions of *Sauromalus* is its habit of folding the forelimbs across the ventral surface at all temperatures below those permitting locomotion. This is a unique habit among the species that have been studied, and may be correlated with its behavior in rock-crevice shelters.

dark colored. This is particularly true of the crocodilians, the larger monitors (*Varanus*), and of the larger iguanids (*Ctenosaura* and *Amblyrhynchus* for examples). It is not impossible that the heat-absorbing properties of dark skins are required to insure the intake of sufficient heat to permit these large poikilotherms to attain temperatures within the normal activity range.

To return to *Sauromalus obesus*, the average range for activity is 37.7° C. This figure was obtained from 25 observations which were made as the animals retreated to shade, and 24 as they retreated underground when shade temperatures became too high. The two series agree to within 0.2° C. The highest temperature recorded for voluntary tolerance was 42° C. The critical maximum appeared at 44.5° C. in one individual, at 49° C. in another, and in a third (under laboratory conditions) at 43.3° C. The reasons for the wide variations are not known. The putative lethal was found to be 50°–51° C. with only four trials, one of them conducted in the laboratory.

Uma inornata and *Uma notata notata*,
Fringe-footed Sand Lizards

Observations on caged *Uma inornata* obtained near Indian Wells indicate a rather consistent refusal to emerge above ground until they have reached a body temperature of 26° C. This coincides closely with conditions found in *Uma n. notata*, observed in the fall of the year.

In the Yuma sand dunes, juveniles of *Uma n. notata* are exceedingly abundant from September to November, and as many as 25 have been captured between 6 and 8 A.M. by the simple process of finger-screening the sand at the bases of the scattered shrubs. (This is not recommended for the novice since the inconspicuous young of the venomous sidewinder are also found in this habitat.)

No lizards were observed above the surface during these hours, or as long as sand surface temperatures remained below 25° C. Within a few minutes after the sand surface (at a depth of 400 mm., the temperature was 30° C. at 6 A.M.) reached 25° C., large numbers of the lizards appeared, and with rising temperatures they became increasingly difficult to capture.

Within a short time after emerging, body temperatures of adults and young rose sharply, and body temperatures of adults during animal activity ranged from 35° to 40.5° C. The average of these temperatures was 38.8° C., and the temperatures obtained from 13 adults taken immediately after capture averaged 38.3° C. with a minimum of 37.5° C. and a maximum of 40.5° C.

Laboratory experiments gave repeated indications of a preference for 38° C., the average being 38.35° C.¹ The average of all data indicative of thermal preference obtained from laboratory, caged, and free individuals is 38.47° C.

Satisfactory data are not available for the putative lethal temperature, but this appears to be close to 45° C.

Sceloporus m. magister, Desert Scaly Lizard

There are no data from either field or cage examples of this species, but one was kept under laboratory conditions for a period of three months and afforded some exceptionally interesting information.

With a choice of air temperatures ranging from 25° C. to 45° C. and with body temperatures averaging 4° C. above those of the air (with the substratum and incandescent light as the sources of heat), the lizard came to rest 41 times out of 53 at air temperatures ranging between 30° and 33° (body, 34°–37° C. [?]). The animal was observed once at 33.5° C. and twice at 25° C.; the balance of the observations were at 28°–30° C.

Just prior to ecdysis the lizard evinced a strong preference for the area where air temperatures ranged between 25°–27° C.

Of greatest interest was the fact that it fed repeatedly with the body temperature at or slightly above 30° C., but that 54 out of 56 fecal pellets were observed where the cage temperature was 35° C. and that of the body 37°–38° C. From these data it appears that the lizards prefer to rest at temperatures slightly below those which lead to defecation.

¹ During the laboratory experiments, lights of different color were used as heat sources. These lizards were least responsive to blue and one animal repeatedly attempted to escape by climbing directly toward the hottest, that is, the closest bulb, the light from which appeared to be dimly visible. So persistently did the lizard return to this spot that it ultimately collapsed from overheating.

Additional work is being conducted on this aspect of reptilian responses to temperature.

Uta stansburiana, Side-blotched Lizard

Owing to the extremely rapid changes in body temperature, changes that are frequently so rapid as to exceed those of which the thermometer is capable, it is felt that the data on body temperatures for the activity range, 35°–38° C., and the lethal, 43.5° C., are no better than close approximations.

Atsatt (1939) has shown that the critical temperature for inducing the light color phase in most of the iguanids ranges from 35°–43° C., whereas *Uta stansburiana stejnegeri*, the desert subspecies, becomes light colored at a temperature of 25° C., or 10°–18° C. below that at which other diurnal desert lizards appear to need diminution in heat absorption. This would seem to indicate sensitivity to high temperatures. Nevertheless, Cole (1943) gives $48.38 \pm 0.26^\circ$ C. as the mean lethal for the subspecies *stansburiana*, almost 2° higher than that of any other species of lizard with which he worked.

The coastal subspecies, *Uta stansburiana hesperis*, is characterized by similar thermal

their preferred habitats, strong differences would be expected. One species, *Phrynosoma b. blainvillii*, is confined to the coastal areas and the higher semi-desert districts of the mountains. Another, *Phrynosoma p. platyrhinos*, has a wide geographic range that includes considerable temperature differences, and the third, *Phrynosoma m'callii*, is restricted to the warmer areas of the Colorado Desert. *P. p. platyrhinos* is found at elevations of 3000 feet, but it is also encountered in the Coachella Valley at sea level or slightly below, where, as at the mouth of the Box Canyon in Riverside County near Mecca, its range overlaps that of *P. m'callii*.

In view of the slight differences in heat economy and the considerable difference in temperature conditions in these habitats, it seems probable that the necessary accommodation to diverse climates is accomplished by means of habits. Coloration and neurological adjustments may also be involved, and it is noteworthy that both of the desert dwelling species are paler in coloration than the coastal form. A comparison of the averages of temperature adjustment at the most significant levels is shown.

	Retreat from Cold	Activity Range	Maximum Voluntary Tolerance	Number of Observations
<i>P. b. blainvillii</i>	28.0° C.	34.9° C.	39.0° C.	26
<i>P. p. platyrhinos</i>	29.0°	36.8°	39.0°	10
<i>P. m'callii</i>	29.3°	36.9°	41.0°	10

requirements. Extensive observations indicate that 26° C. is the minimum temperature at which the lizards will remain active; a drop below this level sends them to shelter. Major activity takes place at 35°–36° C. In the late afternoon when the ground remains warm, activity continues even after air temperatures have dropped below 26° C. When the ground also cools to below this point, the lizards retreat to shelter. In the laboratory this temperature sensitivity has been observed and established to within 1°–2° C.¹

Phrynosoma spp., the Horned Lizards

Little difference in thermal preferences can be detected between the three southern California horned lizards, although, to judge by

From these data it appears probable that a difference of thermal adjustment amounting to only 2° C. distinguishes the coastal species from *P. m'callii*, an inhabitant of the hottest desert areas. This thermal similarity was further emphasized by the observation that sand temperatures of 41° C. or more seemed equally effective in restraining the sand-burrowing impulse. When forced to submerge themselves (pl. 28, figs. 1, 2), however, they all endured short exposures to temperatures as high as 43° C.

As temperatures became unbearable all three species submerged in the sand of their cages, and as the surface layers became hotter they pushed downward until a hard-pan at a depth of 75 to 80 mm. prevented them from penetrating deeper. Under these conditions, usually by 2 to 3 P.M., they would rush to the surface and retreat to the nearest shade,

¹ The senior author is indebted to one of his students, Mr. James Elliot, for the information contained in this paragraph.

where by that time temperatures had moderated sufficiently to be endurable.

Phrynosoma m'callii displayed a greater tendency to crepuscular activity than either of the other species, sometimes remaining above ground for an hour or more after the others had retreated and temperatures in the late dusk had dropped to 29° C. Retreat below ground appeared to be due as much to the light conditions as to the compulsion exerted by a falling temperature.

One of the difficulties involved in obtaining thoroughly reliable thermal records for any given reaction is revealed by the inconsistent behavior of a single example selected at random from among a large number of similar instances. While attempting to obtain data on the minimum temperature at which *Phrynosoma m'callii* leaves the sand on first emergence in the morning, it was noted on one occasion that two individuals resting side by side under apparently identical conditions ultimately emerged at body temperatures respectively 22° and 36° C. Thus there was manifest a difference of 14° C. for a single, apparently spontaneous reaction. It should be emphasized that the lower temperature is well below the level usually tolerated, while the higher figure lies well within the range for normal activity and not far below the limit of voluntary tolerance to high temperature.

Xantusia vigilis, Yucca Night Lizard

As the name implies, this is a nocturnal lizard with a preferred habitat consisting of the dead and decaying debris from yuccas of various species. Where most abundant they are found under the rotting logs of the Joshua tree, *Yucca brevifolia* (pl. 25, fig. 1), although Klauber (1939, p. 98) points out that when *Yucca mohavensis* is also present it seems to be preferred.

Their territorial range extends from Nevada and southwestern Utah, south and west through the Mojave Desert and along the flanks of the San Gabriel, San Bernardino, and San Jacinto Mountains where they are restricted to a narrow belt lying principally at the junction of the Upper and Lower Sonoran life zones. The southerly extensions of their range may be visualized as digitate protrusions penetrating between the hottest parts of

the desert and a cooler, semi-desert, brush-covered area.

The plants for which they have been named follow a similar but less restricted distributional pattern. The Spanish bayonet, *Yucca whipplei*, in which *X. vigilis* has been found at elevations of 4000 feet above Fort Tejon, ranges westward to the coast where it is a common species. Similarly the Spanish dagger (*Yucca mohavensis*) is inhabited by this night lizard on the desert slopes of the San Jacinto Mountains, but along the coast of San Diego County this same plant occurs with the lizard absent. In some localities these lizards are frequently encountered under debris of various sorts or under flakes of rock at considerable distances from these plants. Thus the primary requirements, aside from food and shelter, would seem to be either a definite temperature or rainfall, or a combination of the two. Winter snows are a common feature of their territory (pl. 25, fig. 2).

That the lizards are restricted to areas having modified desert climate is apparent. However, their secretive habits limit them to a special localized climate which will make an understanding of the micrometeorology of their particular niche essential to knowledge of their exact requirements. In winter the temperature under Joshua tree logs inhabited by these lizards falls to as low as 5° C. (air temperatures -7° C.). During the day the temperature may rise to 10°-16° C. In spring (April-May) there are occasions when the temperature under the logs drops to as low as 10° C. but rises to 20° C. and probably higher sometimes at noon.

As late as mid-June (June 18, 1943) the evening temperature under logs which have been shaded during the afternoon ranged from 27.5°-28° C., and those subjected to continuous solar heat radiation throughout the day ranged within 2° of 31° C. At a depth of 2 inches the unprotected soil was 35° C. At sunrise the average temperature under 10 logs was found to be 22.6° C., but by noon (air temperature 32° C.) temperature under shaded logs averaged 30° C. (29°-31° C.) and those in the sun 35° C. (29°-37° C.). The tempering effect of these soft fibrous masses of insulating tissue is apparent. Moreover, it is obvious that there is little correlation between the fluctuations of the meteorological

conditions as usually recorded and the conditions found in the micrometeorological environment.

The lizards are capable of righting themselves from the supine to normal position at 7°–10° C., and they can walk at 11° C. When allowed to select their preferred air temperature in the laboratory, the average of 26 choices was 29° C., with a range of 23°–33° C. Female lizards maintained at temperatures of 27°–32° C., with a mean of 30° C., give birth to young at the same time as those in the wild state (Cowles, 1944), suggesting 30° C. as approximately the optimum temperature. Cole's (1943) conclusions concerning the relative importance of air versus substratum temperature make it difficult to evaluate the above figures regarding thermal preference. However, as noted previously under *Sceloporus*, the body temperatures of the night lizards were probably slightly above those of the air.

During the course of other experimentation it became necessary to establish the lethal temperature for this lizard, and the data assembled in gaining this information are of interest. Six lizards were employed in each of

the following determinations except as noted, and in the last experiment more than 50 were used at one time or another. Substratum and air were heated to the same temperature, which remained constant to within $\pm 0.5^\circ$ C.

All killed in 25 minutes at 45° C. (Without water.)
3 of 6 killed in 1 hr. 15 min. at 40° C. (Without water.)

All killed within 12 hours at 39.5° C. (Without water.)

All killed within 12 hours at 39° C. (Without water.)

2 out of 6 dead in 29 hours at 38° C. (Without water.)

10 out of 12 survived for 4 days at 38° C. (Supplied with water.)

1 out of 10 dead in 8 days at 37.5° C. (Supplied with water.)

All alive at end of week at 36°–36.5° C. (Supplied with water, repeated experiments.)

From these results it is clear that the fatal temperature lies between 38°–39° C., and that water losses may be an important factor. A week at a temperature of 36.5°, with fluctuations of no more than 0.5° C., produces sterility in the males (Cowles and Burleson, 1944).

SNAKES

Coluber flagellum piceus, Red Racer

The lowest temperature at which voluntary activity was observed in this species was 21° C. From behavior observed in the cages, 24° C. may be considered the normal lower thermal limit for surface activity. Their presence above ground at lower temperatures probably indicates unusual excitement or forced activity, and it has been noted that sexual excitement continues to operate in caged individuals at temperatures as low as 23° C. Normal activity without the effects of unusual stimuli was observed only between 27° and 35° C., with rare exposure to a body temperature of 37° C. When not driven by the urge to escape or by other stimuli, there seemed to be a marked preference for temperatures around 33° C. Under laboratory conditions death occurred at 44°, 44°, and 42.4° C.

This is the only diurnal snake that has been studied for thermal reactions. Klauber (1939,

p. 39) reports this snake to be exclusively diurnal and we have found it most active either before or following the hotter part of the day (at times sufficiently late in the evening to be called crepuscular). Consequently it is not astonishing to find the species exhibiting a strong preference for temperatures slightly above those of the nocturnal species.

Phyllorhynchus decurtatus perkinsi, Desert Leaf-nosed Snake

These snakes display acute discomfort at 36.5° C. The critical maximum is reached for subadults at 38° C. (one out of the six used in the experiment showed symptoms of heat damage at 37° C.), but continuous exposure to a body temperature of 36° C. for a period of two hours eventually brought death to all six. In each instance, as respiration became faulty, there was a sharp rise in the body temperature, which eventually rose to 39° C.

A difference of 6° C. was observed between body and environmental temperatures when body temperatures were 34°, 37°, and 38° C.

Laboratory experiments with two large adult individuals gave a critical maximum of 37.7° and 41° C.

***Arizona elegans occidentalis*, Western
Glossy Snake**

Burrowing snakes are difficult creatures with which to work, and consequently there is little available information on the activities of this digging species. Although it is one of the commoner snakes collected while driving at night, in captivity it was secretive and seldom appeared above ground except for intervals of relatively short duration. Like any true burrowing snake, it seems capable of flowing into and out of the loose desert soil with very little locomotory difficulty. Surplus heat acquired during active periods on the surface is rapidly lost by direct conduction when these animals burrow.

The lowest temperatures at which this species was observed above ground were 14° and 18° C. These appearances were exceptional, and surface activity was of very short duration, probably not much in excess of a few seconds. At 19°–20° C., appearances become more frequent, and it is probable that this constitutes a normal lower limit for voluntary surface activity. As stated previously, strong stimuli such as fright or those involved in sexual activities frequently result in modifications of other normal responses.

When glossy snakes were confined in the same cage with *Crotalus cerastes* and *Rhinocheilus lecontei* there were no marked differences in their responses to temperature. With respect to light, however, *C. cerastes* was more tolerant than the other two species. Apparently these three snakes are all relatively cold-tolerant reptiles. Klauber (1939) lists *C. cerastes* and *Rhinocheilus* as the snakes having the appearance of greatest tolerance to low temperatures, and we would include *Arizona* in the same category upon the basis of our observations.

One of the difficulties besetting the acquisition of exact thermal data is the ability of the burrowing snakes to glide into the soil with no preliminary warning of the approach

of a change in behavior. On one occasion, as temperatures fell rapidly, eight of the burrowing snakes were moving about the cage shortly after dusk. As their disappearance was anticipated at air temperatures of 19°–20° C., and body temperatures were desired, the observer was ready to grasp the snakes as they started to descend into the soil. As frequently happened, there was almost simultaneous retreat, and before the snakes could be extricated some seconds' delay had occurred. Because they had already been immersed in what at the time were the warmer, deeper layers of the soil, and would be expected to yield erroneous data, the attempt was abandoned. However, a *C. cerastes* in the same cage, which retreated at the same time and was halfway down the mouth of its open burrow, was seized and the temperature recorded as 20° C. It is probable that the somewhat higher temperature represents heat absorption from the substratum, and that the other snakes would have shown the same temperature at the time of their departure.

Under laboratory conditions these snakes reached their critical maximum at 42, 42, 41, 42, 43° C., mean 41.8° C. Putative lethal temperatures were 43°–44° C. (six observations).

Despite the normal avoidance of both light and high temperatures, these snakes occasionally bask on the surface of the ground in winter, and in summer a large gravid female was captured in Coachella Valley, July 7, 1940, at 8 A.M. in full sun. The day was cloudless and hot, probably well over 38° C. in the shade. To judge by the tracks in the sand, the snake had been very active, presumably during the night and early morning, boring in and out of the ground near a large hummock of earth. It was probably seeking a suitable spot for oviposition. She deposited 23 eggs the following day, and these hatched after 68 days of incubation at room temperature, which fluctuated between 25° and 32° C. At eight days of age, the young were tested for the critical maximum and responded at 38°–39° C. All recovered but showed varying degrees of partial caudal paralysis. Thus the young appear to suffer from temperatures 3°–5° C. lower than those which would be fatal to the adults.

Chionactis o. occipitalis (Sonora *occipitalis* auct.),
Shovel-nosed Ground Snake

Like the preceding subterranean snakes, this species makes short forays above ground and is limited by approximately the same thermal restrictions that apply to other snakes. It is rarely abroad or active under conditions where its body temperature cannot be maintained at 20° or above.

The highest voluntarily accepted temperature observed within the cages was 31° C., but Klauber (*supra cit.*) has reported the presence of these snakes on highways at air temperatures of 33°–34° C.

Under natural conditions the critical maximum for this species is approximately 37° C., with recovery appearing at 33° C. Under laboratory conditions the snakes lost coordinated action at 38° C.

Crotalus atrox (C. *cinereus* auct.), Western
Diamond Rattlesnake

Freshly captured individuals have been observed moving about at 14° C. but this was presumably the result of abnormal stimuli; activity at this low temperature may be ascribed to the presence of abnormal environmental factors. Even at 18° C. there is some activity, but it is limited in frequency, and it is not until temperatures of 27°–30° C. are encountered that the snakes are persistently active. A temperature of 39° C. was observed in the only test for the critical maximum, and this is probably somewhat lower than should be expected.

Crotalus cerastes, Sidewinder Rattlesnake

This small snake bears a general thermal resemblance to *Crotalus atrox* but is somewhat more tolerant of cold. In the cages it was not infrequently active at temperatures of 16° C. When aggravated into doing so, it could carry on a slow though effective locomotion by both the caterpillar method described by Mosauer (1933) and by sidewinding. Normally, activity is not initiated until temperatures between 17.5° and 19.5° C. are attained. Lowe (1943) has reported mating activity as taking place at temperatures between 18° and 20° C., following a night when air temperatures dropped as low as 14° C. Since this was observed in the fall of the year, subsurface temperatures were considerably higher

than those on the surface, and the animals may not have been exposed to body temperatures lower than 20° C.

One of the more interesting characteristics of this snake is its habit of coiling near the mouth of a burrow, in which position thermoregulation is maintained by exposing greater or lesser amounts of the body to direct solar radiation. By this means it is capable of maintaining an almost constant temperature at the preferred or optimum level. Under these conditions the body temperature was repeatedly found to vary between the limits of 31° and 32° C., with a mean of 31.4° C. The maximum tolerated temperature recorded in the cages was 34.5° C. When forced to do so these snakes endured body temperatures as high as 37° C. This was observed experimentally by frightening the snakes into the open and taking their temperatures when heat drove them back to shelter in spite of additional frightening gestures. The critical maximum is reached at a body temperature of 41.6° C., while death has resulted from a body temperature of 42.5° C.¹

Air temperatures of 42° C. cause moderate discomfort. Of greater interest is the fact that body temperatures from 6°–10° C. below those of the surrounding air have been recorded, although absorption of heat by a cooler substratum may have been a factor involved in these records. The infrequent discovery of these heat-sensitive nocturnal snakes coiled fully exposed to the midsummer sun is difficult to explain. On all occasions when they have been discovered under these conditions it has been noticed that the body is much depressed and in intimate contact with the substratum. From the tracks and other observations it has been evident that the animals reached the bedding down place before sunrise and that they had edged the soil from under their bodies (pl. 26, figs. 1, 2). Under these conditions the extensive and intimate contact of the body with the substratum may have accounted for considerable heat absorption by the underlying sand.

¹ Only one Pacific Rattlesnake, *Crotalus v. oreganus*, a species from the colder mountains and coast, has been tested. This gave the critical maximum as 38.8° C. and the lethal as 41° C. It is noteworthy that this dark, sometimes very black, colored species does not occur on the desert. Its preferred habitats lie chiefly in the Upper Sonoran and Transition zones, although its range extends into the Boreal.

TABLE 1
SUMMARY OF BODY TEMPERATURE RECORDS, CONTRASTING DIURNAL LIZARDS WITH SNAKES
(Temperatures in degrees centigrade)

	MINIMUM VOLUNTARY TOLERANCE	AVERAGE OF NORMAL ACTIVITY RANGE	MAXIMUM OBSERVED VOLUNTARY TOLERANCES	CRITICAL MAXIMUM	RECOVERY	LETHAL	COMMENTS
DIURNAL LIZARDS							
<i>Dipsosaurus d. dorsalis</i>	27.0°	37.4°	41.0°	47.5°	43.0°	50.5°	See note regarding reliability of lethals
<i>Crotaphytus wislizenii</i>	23.0	37.4	—	—	—	—	
<i>Crotaphytus silus</i>	—	38.7	41.0	—	—	—	38.7 = probable optimum
<i>Sauromalus obesus</i>	27.0	37.7	42.0	45.6	42.0	50-51	See note regarding reliability of lethals
<i>Uma n. notata</i>	26.0	38.5	40.5	45.0	—	—	38.3 probable optimum
<i>Phrynosoma b. blainvillii</i>	28.0	34.9	39.0	46.7	—	48.0	See note regarding reliability of lethals
<i>Phrynosoma m'callii</i>	29.3	36.9	41.0	—	—	—	
<i>Phrynosoma p. platyrhinos</i>	29.0	36.8	39.0	—	—	—	
Mean for diurnal lizards	27.4	37.3	40.5	46.2	42.5	49.5	
SNAKES							
<i>Coluber flagellum piceus</i>	24.0	33.0	37.0	—	—	42.4	Principally diurnal See general account
<i>Phyllorhynchus d. perkinsi</i>	24.0	—	—	38.0	31.0	39.3	Principally nocturnal
<i>Arizona elegans occidentalis</i>	19.0	27.0	—	41.8	—	43-44	Principally nocturnal
<i>Chionactis o. occipitalis</i>	20.0	—	—	37.0	33.0	—	Principally nocturnal
<i>Crotalus atrox</i>	18.0	—	—	39.0	—	—	Principally nocturnal
<i>Crotalus cerastes</i>	17.5	31.4	—	41.6	34.5	—	31.4° C.—probable optimum Principally nocturnal
Mean for snakes	20.4	31.1	—	39.5	—	41.5	
Difference between means for snakes and for lizards	7.0°	6.1°	—	6.7°	—	8.0°	

DISCUSSION

REPTILIAN ADJUSTMENT TO THERMAL REQUIREMENTS

AS SUGGESTED EARLIER, one of the seemingly important requirements of reptiles is an effective extension of both their daily and seasonal hours of activity. This necessity constitutes a problem which is greatly accentuated in desert regions of the temperate zone.

A notable effect of color change is the extension of available time for normal activity in marginal thermal intervals occurring at dawn and dusk, as well as during spring and fall. Dark coloration expedites heat absorption and thus provides a means of obtaining an appreciable increase in the number of minutes per day during which body temperatures attain optimum or near optimum conditions. Thus, although a body temperature of 27° C. represents the lower limit of thermal activity for some diurnal lizards, soil and air temperatures below this level may be offset by heat absorbed from the sunshine. A lizard living under such a marginal condition will be active on days and at hours when, without an effective heat-absorbing mechanism, it would be incapable of continued activity. The reverse of this condition results from their ability to become lighter in color under bright light. At and above optimum temperatures this faculty provides the animal with effective protection from rapid overheating which would also curtail the time available for feeding and reproduction.

Light coloration in the presence of sunshine can be considered a provision for an appreciable extension of activity during portions of the day when solar radiation and high soil temperatures would limit activities of an organism of dark coloration. The aggregate effect of these extensions of time at opposite ends of the thermal environment must constitute an important element in adjustment to the environment, whether in deserts or even in more temperate areas.

It has already been noted that fatally high temperatures will be reached in reptiles after exposure for a few minutes to spring or summer solar radiation and also that none of the desert reptiles can be considered notably resistant to the great heat of the desert habitat. For these reasons it is not altogether

startling to find that the lizards possess a crude sort of cooling mechanism and that evidence for the existence of such a device is often displayed. Under emergency conditions, that is, on those occasions when circumstances beyond their control force them to exposures which elevate body temperatures to or above the point of comfort, heat is dissipated through rapid respiration and the concomitant increase in evaporation (pls. 27, 28). Deserticolous reptiles can ill afford the loss of water, but it should be noted that thermoregulation through evaporation is most effective in dry regions. Cole (1943) states that under comparable conditions of heat "the lizard in the higher humidity always showed a more rapid rise in temperature."

This type of thermal control is initiated as body temperatures rise above the optimum, and the control is maintained until just prior to death when respiration ceases. As a result of loss of thermal control at death, body temperatures continue to rise sharply until they have attained a maximum having nothing whatever to do with the actual lethal point. This maximum would be identical in similarly colored snakes and lizards, a factor which may have led Mosauer (1936) to the conclusion that there exists no significant difference between the thermal tolerances of diurnal lizards and nocturnal snakes.

As noted elsewhere, thermal control achieved through respiration, and probably other factors as well, ranges from 2°-3° C. to as much as 10° C. under extreme conditions of forced exposure to dangerously high environmental temperatures. However, normal behavior seldom requires such extreme physiological control. Reptiles either retreat from exposure, or under extreme conditions they adopt other methods of avoiding drains on their moisture content which would inevitably result from cooling or evaporation. In this connection, it should be noted that subsoil moisture may be a factor involved in cooling by direct conduction in the case of burrowing forms and perhaps in rodent burrows as well.

It is entirely possible that water losses due to the necessity of lowering temperatures by

evaporation may be one of the major factors which drive these desert animals to retreats underground during the summer months. It seems improbable that heat alone could account for the apparent non-use of night and early morning hours. Activities that are related to conservation of moisture may easily be confused with heat effects. Noteworthy is the fact that the desert-dwelling Gila Monster, *Heloderma suspectum*, in captivity often selects a pan of water when provided a choice of environments.

The part played by relative humidity in thermal control by respiration must be great, but insufficient data for analysis and interpretation are available at the present time. However, attention should be called to the extremely low relative humidity found at ground levels during daylight hours. This has been shown in the graphs prepared by Mosauer (1936). Certainly nowhere but in deserts, where cooling is most necessary, would such propitious conditions of relative humidity of 6 to 20 per cent be found during that part of the day when most needed.

Most desert reptiles are capable of making their own underground retreats, or they may be limited to the construction of small lateral tunnels leading from larger rodent-made burrows. However, in many instances, notably in those forms inhabiting gravel, sand, or other sorts of soil, such reptiles as *Dipsosaurus*, *Crotaphytus silus*, *Crotaphytus wislizenii*, and *Cnemidophorus t. tessellatus* seem to be capable of making their own, sometimes rather extensive, retreats.

Whether self-made, shared, or merely pre-empted, underground shelters or rock crevices are absolutely essential to reptilian survival on the deserts, since no species is capable of surviving exposures to even diffused summer sunshine for more than a relatively short time. As a result of this dependence on underground shelters, the desert poikilotherms are essentially troglodytic during a large part of their life. The existence of diurnal desert reptiles is directly dependent on prolonged and intense radiation, but paradoxically their survival is just as rigorously dependent on their ability to escape from these conditions. The only completely effective sanctuary under conditions of maximum desert temperatures is under ground or in the deeper rock fissures.

Thermal control through behavior is one of the outstanding characteristics of the desert reptiles. Diurnal species often rely on their orientation in relation to the sun to increase or decrease thermal changes due to radiation. When the spring and fall environmental temperatures approach the minimum, the lizards will be found resting in such a position as to expose a maximum surface to the sun's rays. As temperatures approach the effective activity range, the animals are released from the impulse to bask. Only then are they free to engage in their normal activities which continue, regardless of exposure, to a point at which the optimum is achieved. Above this point the body orientation is frequently such as to expose progressively less area to radiation. Nevertheless the animals periodically retreat to shade. Ultimately they are forced to retreat to their burrows, where for a time they remain with only a portion of their bodies exposed. Whether they are submerged in the sand (see pl. 29) or in a tight-fitting burrow, considerable heat must be dissipated through direct conduction. The sidewinder and other snakes adopt a somewhat similar basking procedure and may expose their heads or a part of a body loop and the head, or a loop alone. In lizards it is usually the head only that is exposed to the sun. If environmental temperatures continue to rise, however, desert reptiles retreat still more deeply underground.

As yet no fixed orientation can be correlated with any given body temperature, but repeated observation discloses the following general picture of thermal maintenance through behavior.

Under conditions of unfavorably low ground temperature, the positions that are assumed by lizards vary according to the position of the sun. In the early hours the exposure is dorsolateral, but with occasional dorsal exposure, usually with tail toward the sun. The position is maintained with the anterior end elevated slightly. The entire body is usually inclined in such a position as to achieve reception of the incident light rays at right angles to the body. During cool or cold midday hours, when the substratum is warmer, the body is usually flattened on the ground in order to obtain the same effect.

As temperatures rise toward the maximum,

the sun is faced in such a manner as to expose only a minimum surface to the incident light and heat, and this attitude is also modified at maximum thermal levels by elevating the body. Frequently the tail and toes are also above the ground. In this manner the animals present a minimum absorptive surface to the sun's rays as well as minimum contact with the superheated ground. In rocky country, lizards frequently lie in the shadow of a stone, with only their heads protruding into the sunshine. This habit in some manner may be correlated with the coloration of the black-headed chuckawalla of the Colorado Desert, but whether it is to be interpreted as protective coloration or thermoregulation is a matter of conjecture.

The presence of lizards on rocks "too hot for the hand" and on sand at temperatures of 50° C. and more results from their ability to make short sallies into the open for food, in search of a mate, or in order to scrutinize an intruder. Undoubtedly many of these observations have resulted from seeing lizards which have been flushed from cover by the threat of danger. In any event, the duration of exposure is determined by two factors: intensity of the heat and the volume of the lizard. The adult chuckawalla, *Sauromalus obesus*, on account of its greater volume, seems to be capable of remaining exposed for a longer period than any other species of lizard inhabiting the American Southwest. In contrast the small *Uta* makes only momentary appearances during exceedingly hot days.

The acquisition and maintenance of necessary body temperatures are the *sine qua non* of existence for terrestrial vertebrate ectotherms. All other activities requisite for survival of reptilian species seem ultimately to depend upon the maintenance of necessary body temperatures which makes this element one of basic importance. Successful predation by carnivorous reptiles is based on alertness and agility, and these attributes reach maximum efficiency at or near optimum temperatures. Even for the herbivorous types, the attainment of suitable temperatures is imperative, for they must also maintain high body temperatures if they are to function at maximum efficiency during the crucial moments when they must escape their enemies.

"Survival of the fittest" among terrestrial reptiles would appear to be the survival of the warmest in those instances where other factors are equal. In other words, the most successful reptiles probably are those which, by means of their habits, are able to approach a state comparable to that attained by homiothermic animals.

Another factor that may be of considerable importance is the maintenance of active digestion. For both carnivorous and herbivorous reptiles it is possible that the maintenance of normal digestive processes may be partially dependent on the difference between the thermal optima of the intestinal flora and that of the reptile's digestive enzymes. Temperatures too low for reptilian digestion seem to permit the fermentative and putrefactive organs to multiply rapidly and thus render the food unfit for use. This phenomenon is familiar to anyone who has induced a snake to consume a large meal and has then maintained the animal at temperatures below those necessary for rapid digestion. No experiments on the effects of heat on reptilian enzymes have been reported. However, it is known that amphibian enzymes respond to increases in temperature in a manner similar to most biological functions. Digestive processes may cease, but the putrefactive state of the undigested body leaves no room for doubt as to the continued activity of putrefactive organisms.

Reproduction, both in the initial steps involved in courtship and copulation and in the later stages of gestation and incubation, is also dependent on the attainment and maintenance of suitable temperatures.

In view of the importance of thermal requirements in reptilian survival, it is essential to consider this factor as it exists for the desert ectotherms under the varied conditions to which they have become adapted. Desert animals achieve three great advantages through the acquisition of the fossorial habit: (1) shelter from the vicissitudes of climate by avoidance of high surface temperatures as well as by rapid loss of surplus heat through direct conduction; (2) sanctuary from non-digging enemies of larger size, particularly avian enemies; and (3) the acquisition of a food supply unattainable by non-burrowing forms. Of these three, thermal regulation achieved by selection of optimum tempera-

tures at various depths in the subsoil is perhaps the most important.

As has been described elsewhere (Cowles, 1941), the burrowing shovel-nosed ground snake, *Chionactis o. occipitalis*, and the western glossy snake, *Arizona elegans occidentalis*, ordinarily emerge only at night. During the daytime these animals find suitable diurnal temperatures, as well as the desired complete darkness, just below the surface of the soil. During early spring this thin, sun-warmed crust provides the only thermally satisfactory habitat for photophobic species of poikilotherms. Nocturnality without recourse to underground shelters is not known to exist in the reptiles of the desert areas in the Southwest. The sidewinder, *Crotalus cerastes*, and the diamondback rattlesnake, *Crotalus atrox*, are not known to dig holes, but both resort to burrows made by other animals.

Without accessible underground retreats, it is doubtful if nocturnality would be advantageous to any desert reptile. Obviously, prolonged exposure to summer heat, even in dense shade (seldom available on deserts), would frequently raise the body temperature high enough to cause the death of nocturnal as well as diurnal species, even though the latter are relatively thermophilic. Nocturnality adopted in conjunction with utilization of underground retreats is the only course open to animals that must evade exposure to excessively high environmental temperatures. The advantages of this method of living are enhanced by the correlated conservation of moisture which attends nocturnality and the use of underground shelter. The hottest and driest portion of the day is spent below ground where temperatures are moderate and the relative humidity is higher. At night lower temperatures as well as a sharply rising humidity would tend to conserve moisture.

The advantages of these habits are so evident that it is astonishing that a larger proportion of ectotherms living in hot climates have not adopted a completely subarenaceous mode of existence. Conversely the penalties that would be imposed by a cold climate suggest that only a continuously warm climate over a long period of time could have permitted this development. Indeed the number of burrowing reptiles inhabiting the Southwest perhaps offers confirmatory evidence of

the antiquity of the region as a warm, low desert. It is probable that most species evolved *in situ* from old North American stocks that invaded the region in Miocene times or earlier. Data assembled by palaeontologists and palaeobotanists offer strong evidence that the Southwestern deserts were already coming into existence as semi-arid, perhaps savanna regions by the end of the Oligocene. Since then the history of the region has been one of increasing aridity, with occasional pluvial periods but with relatively little change in the climatic trend. Even during the four glacial advances of the Pleistocene, climates in the Southwest seem not to have been appreciably colder.

Presumably the less adaptable reptiles have failed to survive in desert regions because of the rigorous climatic conditions. Conversely, relicts are more often found on islands and peninsulas owing to the relatively slight temperature fluctuations characteristic of maritime climates. Schmidt (1943) has recently discussed peninsular life and "paleo-peninsulae," pointing out that, "The common faunal characteristic of the major peninsulas is their accumulation of peculiar forms of life, frequently primitive." It has often been hypothesized that insular and peninsular relicts survive because they are relieved of "competition with modern elements," or because "biotic pressures are reduced." On the other hand other authors have spoken of the "extraordinary congestion in species" on peninsulas. Can an abundance of species lead to diminution of competition?

We are inclined to doubt that biotic competition is greatly reduced on peninsulas. Palaeobotanists have established the fact that the southern half of the United States and the west coast as far north as Washington were occupied during the Eocene by a hardwood forest which verged toward the tropical. According to Chaney (1940), the isoflora during the early Tertiary were approximately 10° of latitude farther north. Hence the herpetofauna of the early Tertiary of Middle America existed in what must have approximated a subtropical, equable climate. The gradual shift to a continental climate inland has forced the less adaptable stenothermic reptiles to the coasts and southward on three peninsulas, Florida, Mexico, and

Baja California, as pointed out by Schmidt (*supra cit.*). Moisture as well as heat requirements are undoubtedly involved, but primitive reptiles have survived on each of these because of the less rigorous climates that prevail. The amphisbaenid genus *Rhineura* during the Oligocene ranged northward to South Dakota; today it is confined to Florida. Other amphisbaenids occur in Baja California and in Mexico, but none occurs in central United States. Significantly no monotypic reptilian genera occupy restricted ranges in the middle of the country; the primitive species all occur on the coasts or peninsulas. Relicts include *Anniella* in California, *Bipes* in Baja California, and *Neoseps*, *Liodytes*, and *Stilosoma*, as well as *Rhineura*, in Florida. Numerous other stenothermic groups are restricted to the coastal lowlands of Mexico, and to the Gulf Coast of the United States, where moisture may be a secondary requirement. It is not impossible that desert reptiles survived moist interglacial periods with impunity, as indicated by the presence of desert reptiles in short-tree forest associations in extreme southern Sonora today.

Many modern distributions possibly can be interpreted in terms of thermal and moisture requirements when these are better understood. It must be borne in mind that the principal climatic areas of today probably were in existence prior to the Pliocene. During the late Quaternary seasonal changes presumably approximated those of today. As the summer advances, the temperatures of the surface soils rise above the optimum during daylight hours, and most species included in the sand fauna, both invertebrates as well as vertebrates, burrow increasingly deeper. By so doing they follow the vertical drift of favorable temperatures. The resultant concentration or stratification of fauna in favorable thermal zones may be an important factor in the lives of burrowing reptiles, since it results in a concentration of the available food supply in a comparatively narrow thermal zone.

Throughout the entire summer favorable temperatures exist only a short distance below the ground surface. By selecting almost any level in the vertical thermal gradient, representatives of the underground fauna have access to a considerable range of opti-

imum temperatures. At a depth of 1520 mm. (5 feet) the temperatures are slightly below the optimum for nocturnal species, and the most thermophilous reptiles would certainly be repelled by temperatures which are within 2°–3° C. of those known to be too cold for some lizards. In Coachella Valley the maximum observed temperature at a depth of 1520 mm. (5 feet) is 29° C., and this occurs toward the latter part of August; following this date there is a gradual fall in ground temperatures which continues until late winter.¹

It has been widely assumed that the high air and surface temperatures of summer which drive the reptilian population below ground must inevitably induce estivation, but there is as yet no positive evidence that our desert reptiles enter any "summer stupor." Furthermore it is clear that estivation due to heat alone can hardly take place, since cool refuges are always available a short distance below the surface of the ground. The temperatures at 1520 mm. below the surface are so low that they are only slightly above those which could cause prolonged inactivity in some species. It is conceivable that estivation in desert reptiles is physiologically not dissimilar from the hibernating state. Although heat alone would not necessarily drive desert reptiles to a high-temperature estivation, it must be noted that the absence of water near or at the surface might force them to become inactive. In parts of the Southwest more reptiles are ordinarily encountered on the surface after rains, even though the temperature may have undergone no important change.

The adoption of nocturnal habits alone, without the acquisition of modifying associated attributes, would at once subject a desert ectotherm to a serious limitation in the number of hours available for normal activity. During early spring the temperature limitations of photophobic ectotherms would limit them to an active period of only one or two hours each evening. Even provided this short interval supplied ample opportunity for feeding, the temperatures necessary for digestion might not be available to them owing

¹ These data, compiled by Mr. Dewey Moore, were supplied through the generosity of The Government Date Experiment Station, Indio, California.

to the fact that the later hours of the night become progressively colder. During the day-time at this season all but the shallowest retreats are almost continuously colder than desirable, and complete nocturnality would, therefore, seem to entail serious consequences unless mitigating factors are utilized.

of the mouths of their burrows, with portions of their bodies exposed to insolation. These loops function as animated, voluntarily controlled heating elements.

During summer, nocturnalism theoretically permits longer hours of activity than does the diurnal habit during the same period,

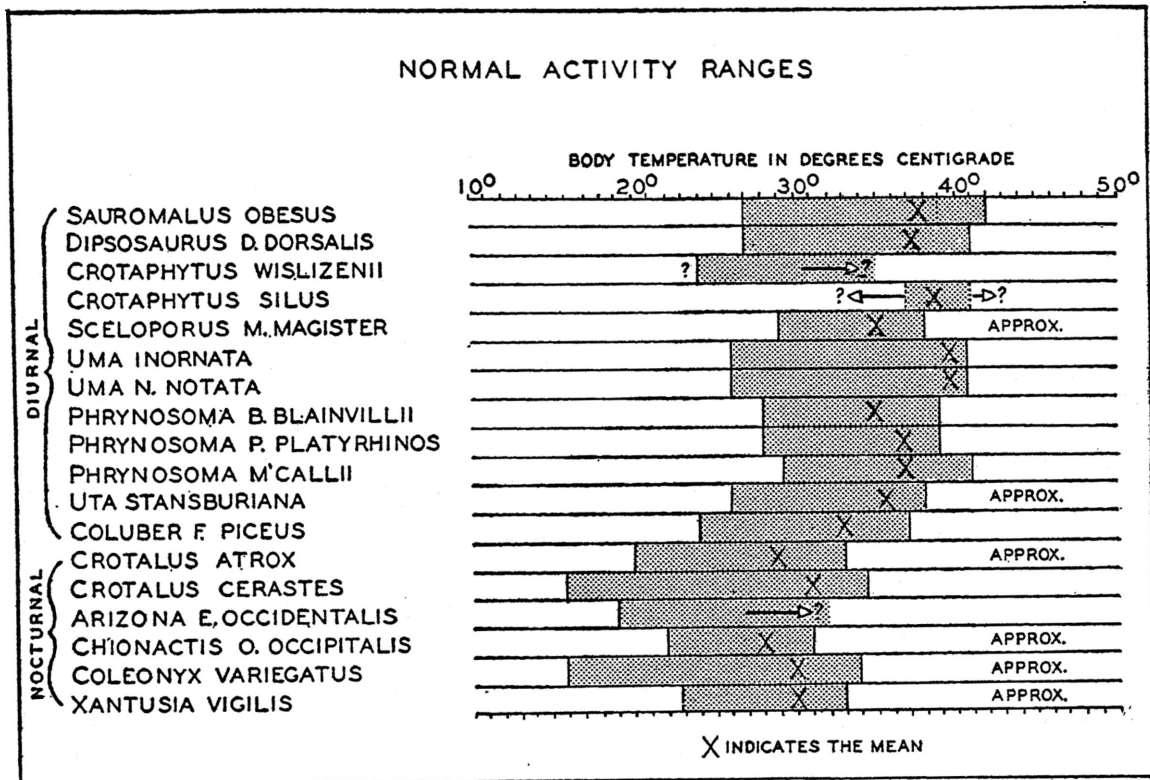


FIG. 3. Normal activity ranges of 18 Southwestern reptiles, including both snakes and lizards. Twelve diurnal forms are arranged roughly in the order of size, with the larger species at the top of the column, and six nocturnal forms are arranged in the same fashion. Stippled portions of the bars indicate the normal activity range, that is, the temperatures between the minimum and maximum voluntarily tolerated by individual species under conditions (1) in the field, or (2) in cages set up in the field, or (3) under laboratory conditions (see text for accounts of individual species). The X indicates the mean for temperatures recorded when individuals were engaged in normal activities, and hence represents an approximation of the ecological optimum. Data for all species are not sufficiently extensive to be considered conclusive. Consequently portions of this chart are provisional, and revisions may prove necessary after controlled experiments in the laboratory have been conducted for the forms in question.

This situation has undoubtedly contributed to a transient diurnalism in some of the non-sand-swimming or quick-burrowing forms. During the early months of spring both the sidewinder, *Crotalus cerastes*, and the diamondback rattlesnake, *Crotalus atrox*, spend much of their time in the partial shade

but, even so, the period of activity would be curtailed, due both to the fact that the nights are short and that all but the early morning hours are frequently too warm for reptilian activity above ground. Curiously, a week of collecting from midnight to sunrise during August resulted in finding only a few diurnal

lizards (males of *Uta stansburiana* and *Calisaurus draconoides gabbi*) and no snakes. This seems to indicate that snakes do not become active at this season, even though temperatures may become favorable.

A resurgence in nocturnal activity takes

place in September and early October, but by November many nights are already too cold for activity, and by late November or early December most reptiles have passed into hibernation.

SUMMARY AND CONCLUSIONS

Twelve diurnal and seven nocturnal species of reptiles indigenous to the Southwest have been studied. Data derived from field observations, from animals in cages set up in the desert, and from supplementary laboratory investigations provide the basis for the following statements:

1. The reptiles under observation were voluntarily active only between the temperature extremes of 16° and 42° C. (cloacal temperatures). Thus the maximum voluntary thermal tolerances of reptiles are somewhat less than those reported for birds. Actually the ecological optimum or the mean for the "normal activity range," as defined herein, is somewhat lower than the normal temperature of many mammals. Consequently even the reptiles inhabiting one of the hottest regions in the world cannot be considered notably thermophilic.

2. Contrary to previous reports, nocturnal reptiles not only tolerate but prefer temperatures somewhat lower than those of diurnal reptiles. Provisionally the difference between mean critical thermal levels for diurnal and nocturnal reptiles may be said to approximate 6° or 7° C.

3. Under captive conditions approximating those in their normal habitats the reptiles studied were able to avoid extensive temperature fluctuations. Particularly noteworthy in this respect was the ability of the sidewinder (*Crotalus cerastes*), while in a relatively inactive or quiescent state, to maintain its body temperature within the narrow limits of 31° and 32° C. The acuity of temperature discrimination in this species under such conditions is astonishing, more especially because the sidewinder proved to be one of the least stenothermic reptiles investigated. Individuals in an active state were noted with temperatures varying from 16° to 34.5° C.

4. Observations recorded for one lizard (*Sceloporus m. magister*) indicate that defeca-

tion is most frequent at body temperatures of 37° to 38° C. It is suggested that such temperatures are necessary before peristalsis is possible, although this same lizard commonly fed with the body temperature closer to 30° C. If such precise requirements are widespread among reptiles, it may account for the high mortality rate among captive reptiles in many zoological gardens where animals are maintained under conditions which prevent them from selecting preferred temperatures.

5. One of the notable facts is the close approximation of the maximum temperatures tolerated voluntarily and the critical maximum which immobilizes the animals. A difference of somewhat less than 6° C. between these levels is indicative of the temperature hazards under which some of these animals would exist, were it not for concomitant adaptations, particularly in habits. The utter impossibility of prolonged activity in the full summer sunshine of the desert is clearly indicated by the black-bulb temperature of 87° C. observed as early as May.

6. It is suggested that reptilian relicts tend to survive on islands or peninsulas owing to the relatively slight temperature fluctuations characteristic of maritime climates. For similar reasons such relicts would tend to survive in tropical regions rather than in continental climates of temperate zones where a higher degree of adaptability to temperature fluctuations would be a prerequisite.

7. A notable characteristic of desert reptiles is the rapidity with which these animals absorb heat. Changes are so rapid as to exceed those of the thermometer in the case of small lizards (*Uta stansburiana*). The rapid changes in reptilian temperatures seem to be due primarily to: (1) their lack of effective surface insulation; (2) their lack of hypodermal adipose tissue; (3) their pigmentation, particularly the melanin; and (4) in the

smaller species, to the relatively small volume in proportion to the large heat-conducting surface.

8. Since an important factor in the thermal adjustment of desert reptiles is the surface-mass ratio of the body, it follows that smaller lizards are capable of utilizing very short intervals of favorable exposures (assuming other factors to be approximately equal). In contrast, larger lizards, under favorable conditions of heat, will require more time in which to reach the optimum, but their activities at higher temperatures will be less restricted than those of smaller individuals or species.

9. Although large lizards exposed to solar radiation or to the warm substratum attain temperatures of maximum toleration more slowly (and also dissipate heat more slowly) than small lizards, there is no apparent correlation between body size and the maximum temperature voluntarily tolerated. Even though the largest diurnal lizard used in these experiments (*Sauromalus obesus*) withstood a body temperature of 42° C. of its own volition, this maximum was closely approached by a much smaller diurnal lizard (*Phrynosoma m'callii*) that voluntarily tolerated 41° C. The data for nocturnal reptiles are not so extensive, but preliminary investigations demonstrate a lower voluntary tolerance.

10. It is apparent that for diurnal lizards the effect of color change (that is, the tint or shade rather than the hue) operates to pro-

vide an extension of time at marginal thermal levels, but the data assembled in these preliminary investigations throw little light on the relative merits of protective coloration versus physiological adaptation. However, a consideration of the size, pattern, and coloration of *Sauromalus obesus* in various regions suggests that some patterns may be interpreted in terms of habits, and that an evolutionary compromise may exist when antagonistic forces are involved.

11. Thermotaxis through behavior is one of the outstanding characteristics of desert reptiles. Body temperatures within the normal activity range are attained principally (1) by selecting positions in or on soil, or rock, where heat through direct conduction can be absorbed, or (2) by basking, with all or only part of the body exposed, to sources of solar heat. Conversely temperatures above the critical maximum are avoided (1) by retreating to cooler depths, in the ground (by burrowing or in preëempted burrows), in rock crevices, or beneath insulating material, (2) or by respiratory cooling under extreme conditions.

12. Because the activities necessary for the survival of both the species and the individual are dependent upon the acquisition and maintenance of suitable body temperatures, thermoregulation by means of behavior may be considered an element of basic importance in the existence and evolution of reptiles in continental climates.

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