HISTORICAL PERSPECTIVE

Preliminary Study of the Thermal Requirements of Desert Reptiles[1]

Raymond Bridgman Cowles and Charles Mitchill Bogert

Preface

Cowles and Bogert's "Preliminary Study of the Thermal Requirements of Desert Reptiles" is something of an anomaly in biology. It is a paper that introduced new concepts concerning an entire vertebrate class and presented a rigorous framework for experimental studies which has survived with remarkably little change for three decades. A major field of herpetological research can be traced directly to the appearance of this work, and for more than a quarter of a century nearly every paper dealing with the thermal relations of reptiles has referred to "Cowles and Bogert 1944."

Cowles had long been interested in the ecology of the reptiles of the deserts of southern California and in 1938 he took advantage of sabbatical leave to set up a field station in the Coachella Valley. His initial interest was the winter activities of reptiles and he gathered information by following a bulldozer that was excavating clumps of mesquite and creosote bush in preparation for irrigation. It was this interest in cold reptiles that first brought him into the desert with a thermometer in his hand. The resistance of reptiles to low temperatures and their ability to resume activity when they were warmed suggested to him that perhaps it was increasing temperatures at the end of the Mesozoic that led to the extinction of dinosaurs via heat-induced sterility. On this basis he suggested that fur and feathers first evolved to keep heat out, not in. From this hypothesis it was a natural step to studying the reactions of living reptiles to high temperatures. The prevailing view at the time held, with impeccable logic, that if a lizard sits on a burning hot rock, the lizard must be as hot as the rock. Biologists marveled at the heat tolerance of reptiles, although there were some hints that reptiles really preferred to be cooler.

The continuing value of the "Preliminary Study" rests on its two major characteristics: it was an entirely new way of looking at the biology of reptiles, and the methods and their application were extraordinarily rigorous. Cowles and Bogert discarded 80% of their body temperature measurements because of uncertainty about the activity of the animal before a measurement was made or because they felt the temperature might have changed during the process of

Continued on page 54

[1] *Bulletin of the American Museum of Natural History* 83:261–296 (1944, reprinted in 1974 by the Society for the Study of Amphibians and Reptiles, Miscellaneous Publications, Facsimile Reprints in Herpetology).

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.

Editor's Note.—Early herpetological literature tended to be of interest to a very limited audience — other herpetologists. Much of the work was focused on listing the species found in particular areas and describing their basic natural history, and an evolutionary perspective, beyond the taxonomic focus, was rare. Perhaps the first herpetological work to break into the awareness of biologists at large was the 1944 publication of "A Preliminary Study of the Thermal Requirements of Desert Reptiles" by Cowles and Bogert, an eco-physiological study with an evolutionary view. The importance of the work stems from the demonstration that "cold-blooded" organisms did not passively take on the temperature of their environment, as previously thought. Instead, Cowles and Bogert were the first to document what we now take for granted: Reptiles have sophisticated behavioral mechanisms that allow them to precisely regulate their body temperatures within a fairly wide range of ambient conditions. This was not the last collaboration between the two nor the final study of reptilian physiology. However, whereas most of the work published that long ago is rarely referenced, the paper excerpted here is still frequently cited, showing its enduring value — sixty years later, this work is still a major milepost.

The original paper is too long to fully include here, as is the Preface by Harvey Pough, added in the SSAR 1974 reprint. I have selected excerpts from both the original work and Pough's preface in order to give readers a sense of the scope of the work, selecting paragraphs that illustrate both substance and style of the work. In the interest of brevity, the bibliography has been omitted, although references were retained in the text (but not in the preface). For those interested in reading more, the SSAR reprint is still available for sale, along with some other historically important herpetological publications. All can be found at www.nbb.cornell.edu/neurobio/department/faculty/adler/not%20using/ssar.html.

Gad Perry, Editor
Texas Tech University

Preface continued from page 53

measuring. The importance of that caution cannot be overstressed. Inanimate objects (in this instance beer cans) distributed through the environment show a distribution of "body" temperatures which resembles the body temperature distribution measured from live lizards. In other words, the observation of a negatively skewed temperature distribution centered about a clearly-defined mean that is higher than air temperature does not demonstrate thermoregulation. It is essential to combine measurements of temperatures with observations of the animals' activities.

The scope of the field opened to investigation by the view of reptiles as animals capable of a considerable degree of homeothermy has not yet been fully realized. In the first place it has made the classic division of animals into homeotherms (warm-blooded) and poikilotherms (cold-blooded) meaningless. During the course of the study Cowles coined the words endotherm and ectotherm to emphasize the source of the energy that warms the body. The realization that reptiles can and do control their body temperature has had ramifications in many areas of herpetology. Ecologists have found that niches are defined in part by thermal relationships, ethologists have discovered that reptiles behave differently at different body temperatures, and zoogeographers must consider the radiant energy regimes available on postulated routes of migration. It is scarcely possible to ask a question about the biology of reptiles in which their thermoregulatory capacities are not directly or indirectly involved. In particular, the very active research in reptilian environmental physiology is built to a great extent around thermal relations and thus stems from the "Preliminary Study."

There has been remarkably little modification of the views embodied in the original paper during more than a quarter century of extensive work. One of the first changes was a de-emphasis of the concept of the "ecological optimum" represented by the mean value of the body temperatures measured during activity. Bogert found that the same genera of lizards maintained very similar body temperatures in different habitats while different genera maintained different temperatures in the same habitat, indicating an hereditary preference for a particular body temperature level. The hereditary preference could be affected by environmental conditions. For example, in Florida, which was frequently cloudy, *Cnemidophorus* body temperatures were skewed toward the lower end of the activity range while they were skewed to the upper end in sunny Arizona. In other words, the activity temperature should be viewed as a range of temperature which is acceptable to a lizard species and allows it to carry on the activities necessary for life. Indeed, a lizard that is kept continuously at the average temperature it selects in a temperature gradient loses weight and may even die. Regal has shown that lizards voluntarily select low body temperatures at night. Apparently different aspects of a lizard's internal economy function best at different temperatures and some temperature variation is essential.

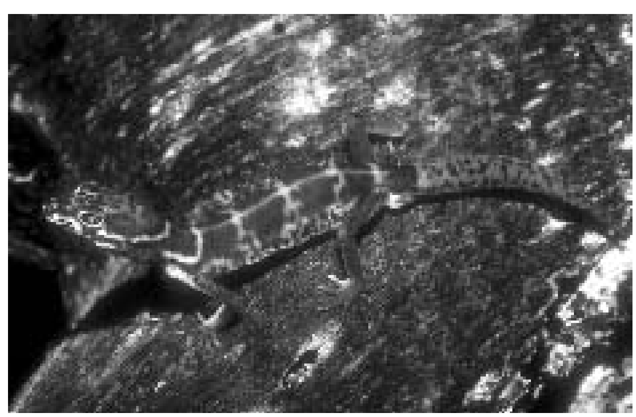
F. Harvey Pough
(excerpted from the 1974 SSAR edition)

This view from Santa Rosa Mountain illustrates several "typical" components of the Coloradan subdivision of the Lower Sonoran life zone.

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.

Methods: 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.

Experimental results (representative species, chosen for diversity and availability of pictures): *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



The thermal responses of nocturnal Banded Geckos (*Coleonyx variegatus*) closely approximate those of nocturnal snakes.

Normal activity of Desert Iguanas (*Dipsosaurus doralis dorsalis*) occurs at temperatures ranging from 34–41 °C.

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 animals 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 invari-


BRADFORD D. HOLLINGSWORTH

Chuckwallas (*Sauromalus ater*, formerly *S. obesus*) do not expose themselves to view until their body temperatures have risen sufficiently to insure an ability to escape a predator.

ably retreated to cover when lowering temperatures approached 23°C. Other observations did not yield conclusive data.

Sauromalus obesus, Chuckawalla. At 14° C. these animals are scarcely able to right themselves from a supine to normal position. 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. 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.

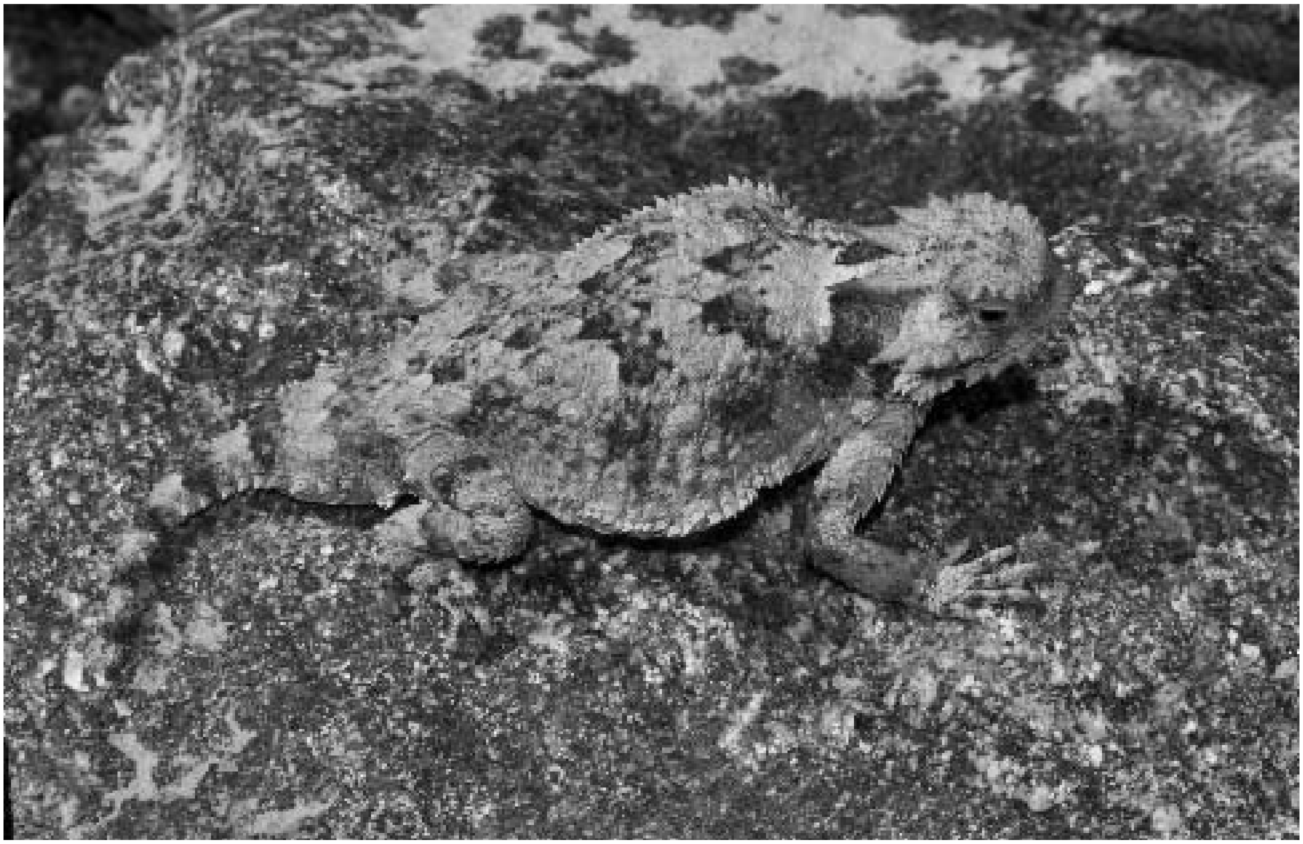
Chuckawallas should furnish an excellent source of information on the importance of color as a physiological adaptation versus its value as a means of concealment. The color variability (but not metachromatism) that is found within any one species of the horned lizard (*Phrynosoma*), fringe-footed lizard (*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. 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 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.

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



Desert Horned Lizards (*Phrynosoma platyrhinos*) have a broad geographic range that includes varying temperature regimes.

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 below.

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, however, they all endured short exposures to temperatures as high as 43° C.

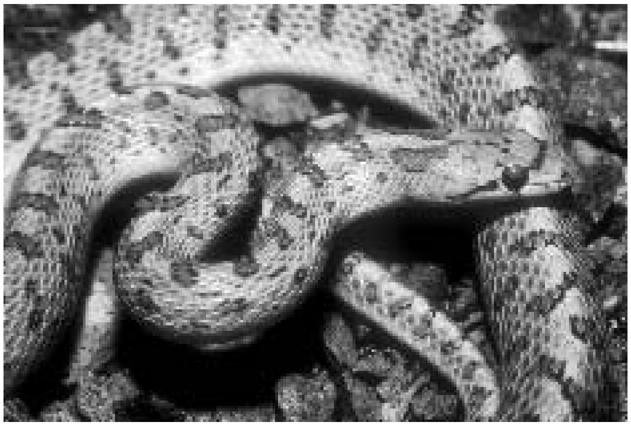
As temperatures became unbearable all three species submerged in the sand of their cages, and as the surface layers became hotter they pushed downward until a hard-pan at a depth of 75 to 80 mm. prevented them from penetrating deeper. Under these conditions, usually by 2 to 3 P.M., they would rush to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

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 secre-

	Retreat from cold	**Activity range**	**Maximum voluntary tolerance**	**Number of observations**
P. b. blainvillii	28.0° C	34.9° C	39.0° C	26
P. p. platyrhinos	29.0°	36.8°	39.0°	10
P. m'callii	29.3°	36.9°	41.0°	10



Glossy Snakes (*Arizona elegans*) are burrowers; any surplus heat acquired during periods when active on the surface is rapidly lost by direct conduction when these animals burrow.

tive 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.

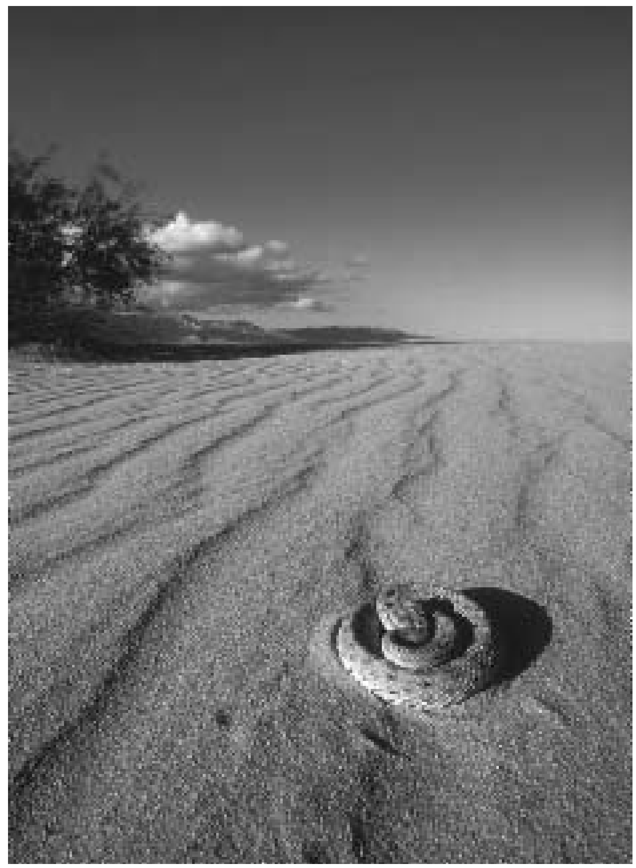
The lowest temperatures at which this species was observed above ground were 14° and 18° C. These appearances were exceptional, and surface activity was of very short duration, probably not much in excess of a few seconds. At 19°-20° C., appearances become more frequent, and it is probable that this 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.

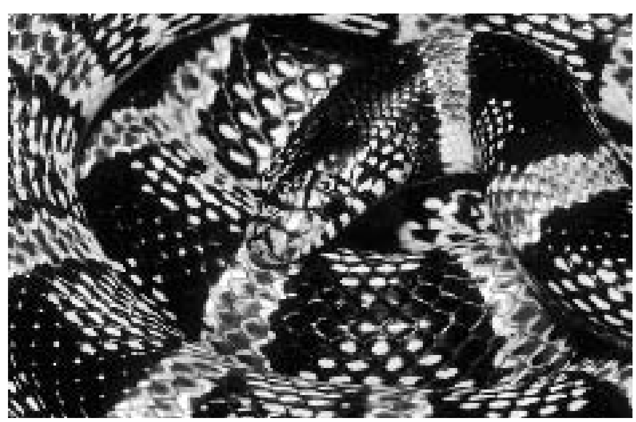
When glossy snakes were confined in the same cage with *Crotalus cerastes* and *Rhinocheilus lecontei* there were no marked differences in their responses to temperature. With respect to light, however, *C. cerastes* was more tolerant than the other two species. Apparently these three snakes are all 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, 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





Sidewinders (*Crotalus cerastes*) and Long-nosed Snakes (*Rhinocheilus lecontei*) are both relatively cold-tolerant, but the former is more tolerant of light than other nocturnally active snakes.

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.

Crotalus atrox (*C. cinereous* 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.

Discussion: 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….

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….

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 "paleopeninsulae," 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 hypothecated 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?...

Many modem 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.

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 arid 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 defecation 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 tem-

perature 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 provide 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 preempted 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.

L. LEE GRISMER

Rapid changes in reptilian body temperatures, especially in smaller species like the Side-blotched Lizard (*Uta stansburiana*) are attributable, at least in large part, to the relatively small volume in proportion to the large heat-conducting surface.