



# University of Arizona

COLLEGE OF AGRICULTURE  
AGRICULTURAL EXPERIMENT STATION

## WATER REQUIREMENTS OF DESERT ANIMALS IN THE SOUTHWEST

By

CHARLES T. VORHIES

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## TABLE OF CONTENTS

	PAGE
INTRODUCTION.....	487
METHODS.....	490
KANGAROO RATS AND POCKET MICE.....	493
THE WHITE-THROATED WOOD RAT.....	503
THE GROUND SQUIRRELS.....	508
THE JACK RABBITS.....	513
MESQUITE FOREST <i>versus</i> DESERT.....	516
SUMMARY.....	523
LITERATURE CITED.....	524

## ILLUSTRATIONS

PLATE I.—KANGAROO RAT AND HABITATION.....	491
PLATE II.—WHITE-THROATED WOOD RAT AND HABITATION.....	505
PLATE III.—JACK RABBITS.....	514
PLATE IV.—INSTRUMENT SHELTERS IN FOREST AND DESERT.....	517
FIGURE 1.—THE MICROCLIMATE OF <i>D. spectabilis</i> FOR ONE WEEK.....	496
FIGURE 2.—THE MICROCLIMATE OF <i>D. spectabilis</i> FOR TWELVE MONTHS....	500
FIGURE 3.—THE MICROCLIMATE OF <i>N. albigula</i> FOR ONE WEEK.....	502
FIGURE 4.—THE MICROCLIMATE OF <i>N. albigula</i> FOR TWELVE MONTHS.....	506
FIGURE 5.—THE MICROCLIMATE OF <i>C. tereticaudus</i> FOR ONE WEEK.....	510
FIGURE 6.—THE MICROCLIMATE OF <i>C. tereticaudus</i> FOR TWELVE MONTHS..	511
FIGURE 7.—SOIL SURFACE TEMPERATURES IN MESQUITE FOREST, AND "CHECK" ON ADJACENT DESERT.....	518
FIGURE 8.—AIR TEMPERATURES IN MESQUITE FOREST, AND "CHECK" ON ADJACENT DESERT.....	520
FIGURE 9.—HUMIDITY IN MESQUITE FOREST, AND "CHECK" ON ADJACENT DESERT.....	521



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## INTRODUCTION

Water is essential to life and during the period of development it is the most abundant constituent of living organisms, its amount ranging from about 40 to nearly 100 per cent of the total weight. Some of this water is imbibed directly, some of it is taken with the solid food which is rarely dry, and some of it is formed within the organism by metabolic changes in the organic constituents of the food and tissues, induced by respiration and other vital processes. The relative amount of water derived from each of these sources depends upon the kind of organism, its period of growth, the nature of its food, its environment, and its activities.

—S. M. Babcock, 1912.

There is hardly a more intriguing or less understood problem of the arid regions of the world than that of the means by which some of the animals of these areas exist without visible sources of water supply. Man must have water to drink, and civilized man inhabits chiefly those areas of the earth where a supply of this necessity is reasonably dependable.

It is, therefore, natural for man to suppose that other animals, especially the higher vertebrates, require drinking water. Also, perhaps the best known popular literature on some of the larger "desert" animals is that of Africa, where, as nearly everyone knows, the larger animals gather at water holes to drink in drought times. When, therefore, we find ourselves living in the midst of a semiarid or desert region, such as southern Arizona, and when we begin to notice that jack rabbits and many other animals seem undisturbed by disappearance of near-by surface water, we are interested and puzzled. Thus the prairie dog, obviously anchored to its villages or "towns" and unable to go miles for drink, was for many years supposed to "burrow down to water." Not until more scientifically minded men determined the actual burrow depth (12 to 14 feet) and pointed out that near the rim of the Grand Canyon, where the nearest water is a "mile down," prairie dogs nevertheless lived contentedly, did we begin to seek another answer.

The scientist or traveler penetrating southwestwardly the progressively drier and drier area of southwestern Arizona (perhaps worried about his own water supply) could hardly fail to notice that there is still some animal life; though the permanent water holes (tinajas) are 30 or 40 miles apart.

Here and there a jack rabbit, even an occasional cottontail, a coyote crossing the trail, a roadrunner, a flock of Gambel's quail, some mule deer, or the once plentiful mountain sheep (desert bighorn) all attest to a remarkable ability to survive with a minimum of water. Closer observation, or more technical acquaintance with the fauna, discloses a relative wealth of small vertebrate life.

The junk-heap nests of wood rats (*Neotoma*) are common, while kangaroo rat (*Dipodomys*) and pocket mouse (*Perognathus*) burrows are abundant. These little creatures are tied to their home burrows and cannot travel even 4 or 5 miles to and from a water hole, to say nothing of a 40- or 50-mile round trip. Such a jaunt might work off more water than the creature could drink.

Thus curiosity is aroused, and the observer begins to think over the problem. The animal *has* to have water for its life processes, but it hasn't any. A paradoxical situation. What is the answer? The number of inquiries we have had, not only from the lay public but from scientists, proves the interest.

But is it important? It may be a trifle difficult to see a direct connection between the answer to this problem and a practical application thereof. Scientifically, it is no less important than any other biological problem in the realm of pure science. Water is the universally necessary major component (by weight) of all living cells, and as such has been investigated from every viewpoint by both plant and animal physiologists. Its relationship to cell activity and life has been long and painstakingly studied and continues to be investigated, and rightly so.

The physiological necessities of the tissues of desert animals as to water are essentially the same as those of animals of moister regions; but the requirements of the animal as an organic unit and the adaptations by which it meets those requirements have not yet been thoroughly investigated.

Buxton, in his volume *Animal Life in Deserts* (1923), brings together a large amount of material on the subject; but the scientific value of his work is much reduced by a total lack of documentation. There is no bibliography, references are undated, and authors are mentioned by surnames only, making it practically impossible to check on the extent and character of the observations, or experiments, if any, on which statements are based.

Sumner (1925) enumerated *Some Biological Problems of Our Southwestern Deserts*. One of his most important suggestions, even yet not adequately investigated, is that of emphasizing the "need of experimental studies upon the special physiology of desert mammals, on a scale comparable with those which have been conducted on desert plants."

Shreve (1934), in *Problems of the Desert*, said:

Relatively little has been done on the water relations of animals. A comparison of the role of water in metabolism in the animal groups of the desert is not yet possible. The loss and requirement have been investigated in relatively few forms. Many desert animals are known to take no liquid water, and our knowledge of their supply through moist or dry food is very incomplete. Terrestrial insects are exposed to higher temperatures than any other animals, but very little is known about their temperature relations and the bearing of these relations on their obviously low water requirements. . . . Some of the most interesting and at the same time complex problems of the desert relate to the plant and animal life which shows itself to be so well adjusted to conditions of great aridity.

Kashkarov (1935) says:

The ultimate aim of scientific study of a desert led on by zoologists and other specialists is to come into full possession of it, that is to promote cultivation, animal husbandry and instalment of a settled population. Desert life conditions must be described and understood for that purpose. The zoecologist must give a description of life conditions in terms of the life process itself.

Such an aim led Kashkarov to a study related in *Ecology of Domestic Animals* (19—),<sup>1</sup> from which investigation he concluded as follows concerning Karakul sheep:

The lambs of the Karakul sheep grow and develop quicker than those of the European sheep . . . [owing to] the shortness of the vegetative period. . . . The fat tail is a reserve of nutritive substance and of metabolic water, and enables the Karakul sheep to live through the winter and to survive the summer drought.

This means that the Karakul sheep is a desert-adapted domestic animal. It might be worth while to try this breed in the Southwest.

Howell and Gersh (1935) carried out some controlled physiological experiments on *Dipodomys* which will be referred to in our discussion of that genus. Further experimentation of this character should be done with pocket mice (*Perognathus*).

The Carnegie Institution Desert Laboratory, at Tucson, was concerned for many years with the water relations of desert plants. It behooves zoologists to learn something of the same sort with respect to animals. It was with this thought in mind and with the object of investigating the water relationships of desert animals that we undertook some years ago a long-time project for the study of this problem.

Our field investigations on mammals (Vorhies and Taylor, 1922, 1933, 1940) offered so much opportunity for general observations and thought on the problem as to foster a desire to undertake field studies rather than laboratory experiments in physiology. Aptitude, training, and the opportunities at hand determined this choice, rather than any failure to recognize the importance of physiological investigations.

The objective of the field investigations was to secure records of the "micro-climates" of certain key species of small mammals of the arid Southwest. We shall have to assume herein that the general characteristics of a desert climate, such as low relative humidity, scanty precipitation, much sunshine and heat, and a wide daily range of temperature and humidity are known to the reader.<sup>2</sup>

The climate of Tucson, Arizona, and the surrounding valley area in which the field records were made is essentially a desert climate, and is typical of a large area of the southwestern United States and northwestern Mexico. It is not of the extreme desert type, and is commonly referred to as "semiarid." Toward Yuma, in the southwestern corner of Arizona, the altitude decreases, the

<sup>1</sup>Reprint, in author's library, without date or indication of original publication.

<sup>2</sup>Buxton (1923) has a good chapter on the desert climate.

heat and aridity increase, and in the Imperial Valley of California and in northwestern Sonora, Mexico, are found the extremes of aridity in the Southwest. The same genera of mammals, with specific differences, occur in this whole area.

In midsouthern Arizona there are two rainy seasons, with intervening dry periods in early autumn and late spring. The late spring, or "arid foresummer" (May-June), is the drier and the hotter of the dry seasons, and therefore the most critical season of the year in the lives of the desert animals. At Yuma, Arizona, and in the Imperial Valley of California there are, typically, but one wet and one dry season, there being no summer rains to break the long, hot season.

It soon becomes evident to the field ecologist that the animals in a desert adjust themselves to the extremes of climate and to the exigencies of food and water supply; and our problem is to determine the extent and nature of these adaptations.

### METHODS

These studies were inaugurated with a battery of climatic instruments set up in and around a typical "mound" of the large kangaroo rat (*Dipodomys spectabilis*) (Pl. I 1). These were located on the Santa Rita Experimental Range, 35 miles south of Tucson, at an altitude of about 3,700 feet. The objective was a series of records of the "micro-climate" of this species.

Housed in standard instrument shelters were: a recording hygrothermograph for air temperature and relative humidity; three soil, or distance, thermographs to record (a) soil surface temperatures, (b) temperatures at "arm's length" within the den, and (c) temperatures at approximately nest location or depth within the burrow. Soil surface temperatures were taken by laying the sensitive bulb in horizontal position half imbedded in the soil. The bulbs almost matched the soil in color. With a good laboratory thermometer a series of checks of the actual temperature of the surface of the soil at various times of day and under a variety of conditions was made and compared with the thermograph temperatures. There was close correspondence. It has been objected that the bulb thus exposed "accumulates heat." Why not? So does the surface layer of the soil accumulate heat. We wanted to know what temperature an animal sitting, lying, or standing on the ground actually encounters. We think we have found out.

Precipitation was measured weekly in a near-by rain gauge. Records were kept at this station from March, 1930, to November, 1931. Then the instruments were moved a short distance, still within a 2-acre enclosure, to the den of a wood rat (*Neotoma albigula*). Here the same installation was used, except for such variations as the differences in dens between the two species required. The soil surface around the kangaroo rat mound is bare; that around the wood rat den generally has some cover of vegetation. A soil thermograph bulb lay just within the wood rat den

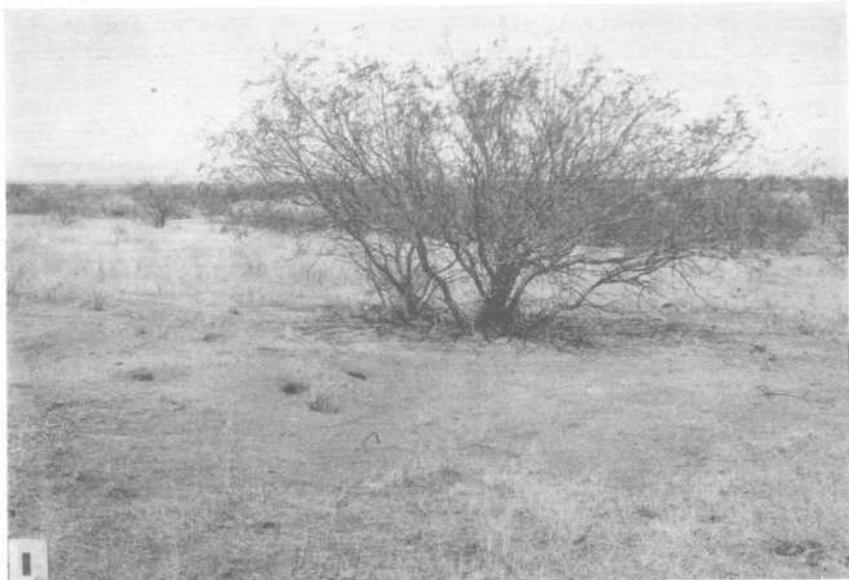


Plate I.—Kangaroo rat and habitation: 1, The home "mound" of *D. spectabilis*, surrounded by a completely bare area. 2, The banner-tailed kangaroo rat, *Dipodomys spectabilis*.

opening, instead of at arm's length within; and another was placed where the nest was judged to be, which is at much less depth than in the kangaroo rat den, and is in a partially open burrow.

Records at the *Neotoma* den ran from January, 1932, to July, 1933. Again the instruments were moved, this time to record conditions at a ground squirrel (*Citellus tereticaudus*) habitation. Since this species is available in abundance much nearer to the Experiment Station, a site was chosen on a corner of unused

ground at the University Farm, 5 miles northwest of Tucson, on the Casa Grande highway. *C. tereticaudus* is somewhat gregarious, and an active colony existed at this location, which is in the Santa Cruz River bottom at an altitude of 2,300 feet. The soil is without vegetative cover during most of the year. Burrows of *Citellus* are deep. The system is complex, and we have not yet succeeded in completely excavating and mapping one. They extend to a vertical depth of at least 3 feet, however. Here the soil thermographs were used to record temperatures at soil surface and at "4 feet depth," which was really at a vertical depth of 3 feet. Since it was not practical to insert the thermograph bulb for such a distance, or depth, into the small and tortuous tunnels, an artificial burrow was substituted. A 4-foot length of 1½-inch diameter radiator hose was buried at an angle to a vertical depth of 3 feet, and the bulb lowered to the deep end. This expedient was only a moderately good makeshift, since doubtless there was more air movement and daily range of temperature at the bottom of the straight tube than at a correspondingly deep point of the natural burrow. This installation was maintained from June, 1935, to the end of October, 1936.

In November, 1936, a new installation for a different purpose was set up on the small ranch of Mr. H. E. Weisner, 8 miles south of Tucson. Here at an altitude of about 2,600 feet, in the Santa Cruz River bottom, was available an area of relatively undisturbed mesquite forest, contiguous to which, and only a few feet higher in elevation, lay the typical "mesa," with its scanty cover of creosote bush (*Larrea*), cactus, rabbit brush, etc., the so-called "desert" of this region. Within the mesquite forest were placed a rain gauge, a hygrothermograph, and a soil thermograph for soil surface temperatures. A duplicate set of instruments was installed in the contrasting desert area.<sup>3</sup> The distance between the installations was only a quarter mile. Records at these stations were begun in November, 1936, and carried until June, 1938, at which time it was intended to discontinue them. However, Lee W. Arnold, a graduate student, took up a field problem (thesis unpublished) on the same area, and the instruments were returned in November, 1938, and records continued into March, 1940.

The records are not in an unbroken series for the periods indicated. Gaps occur when an instrument fails, either through mechanical mishap or failure of the human operator to wind the clocks. A small beetle in the clockwork once meant a gap of some days. The most frequent cause of instrument failure is in the delicate hairs of the recording hygrograph, which may refuse to operate correctly even when reset each week. Although the humidity records are less reliable than the temperature records, it is felt that the general picture of relative humidity is fair. While it was hoped originally to find some means of determining relative humidity within the animal burrows, no satisfactory

<sup>3</sup>Designated "mesquite check" in the graphs.

means was found. There is no "soil or distance" hygrograph for recording relative humidity within the narrow confines of a small rodent burrow. Various small instruments, including a duff hygrometer, were tested for use in securing individual readings of humidity within burrows. Most are unwieldy to insert into the burrow, and all, even the duff hygrometer, are subject to choking up with dirt or gravel. Thus, in spite of the great desirability of making comparisons of relative humidity within the underground habitations of the selected species with the relative humidity records in the open air, it could not be done. All we can do is to point out the practical certainty that, as the logic of the situation indicates, the atmospheric humidity within an underground burrow is definitely higher during the heat of the day than outside. This difference, even when the soil itself is relatively dry, must be physiologically significant in relation to water loss from the body of the animal inhabitant, and therefore to its ability to exist with minimum water intake.

It is believed that the results secured by these methods, correlated with the food-habits studies of Vorhies and Taylor (1922, 1933, 1940) throw considerable light on the problem of the water requirements of desert animals. Hence, an approximate evaluation of the proportions of air-dry and succulent foods in the diets of four types of mammals and their correlation with the respective climatic environments is now attempted. For no one of these four species is there accurate information on the water content of the food, since the exact proportions of air-dry and succulent foods consumed are not known.

#### KANGAROO RATS AND POCKET MICE

Kangaroo rats (*Dipodomys* spp.), pocket mice (*Perognathus* spp.), and related genera of the family Heteromyidae exist and even thrive on a diet with a high proportion of air-dry foods, mainly seeds, with a relatively small proportion of green (succulent) food at such times as the latter may be available. The bases of this assertion are: (1) the overwhelming proportion of dry storage, mainly seeds, in the dens must be indicative of the major food supply; (2) conversely, the paucity of evidence of consumption of truly succulent food either as green vegetation, cactus (pulp or fruit), or bulbs; and, (3) the ability of certain species to live for some time in captivity without free water, on a diet high in air-dry foods, and with a minimum of succulent food.

Buxton (1923) serves in this connection to emphasize the parallelism of both structure and habit between certain rodents of Old World deserts and the Heteromyidae, or kangaroo rats and pocket mice of our southwestern deserts. In Palestine, Mesopotamia, Egypt, the Sahara, East Africa, and in other Old World deserts live the gerbils (*Meriones*, *Taterona*, *Gerbillus*), jerboas (*Dipus*, *Jaculus*, *Dipodillus*), and others which are nocturnal; travel kangaroo-like on two powerful hind legs; live in underground burrows, the openings of which may (or may not) be

plugged against the heat; exist mainly on air-dry foods, such as seeds; and thrive without available drinking water.

Buxton says (p. 82):

I remember an Egyptian jerboa which was kept by a member of my family as a pet. It was given no water and lived for many months on crushed oats and bran; when it was offered apple or carrot or other moist food, it generally refused to eat it. That it could not drink dew is certain because it lived in a London house.

A humid climate, also, we may point out.

The literature relating to the water requirements of desert animals is somewhat confusing, in that seemingly authentic records concerning certain types of animals are contradictory. Buxton follows the above quoted record with: "Cheeseman kept captive specimens of a different species (*Jaculus loftusi*) in Basra, Mesopotamia, in summer, and remarked, that "They drank frequently, taking small sips in their forepaws. This is remarkable, as their earths are often placed where both dew and water would be to all appearances unobtainable!" The hot, dry atmosphere of Basra in summer as against the humid air of London may account for this difference.

The sources from which desert animals obtain their required moisture has long been a moot question. Buxton (*loc. cit.*, p. 82) says: "It is almost certain that many . . . small mammals depend solely upon the minute quantities of water to be found in seeds and dead plants which have become completely 'air-dry.'" But (p. 126), quoting Tristram, he says: "The vast numbers of little rodents in apparent deserts is explained by the nature of their food, which is chiefly supplied by bulbous roots." He mentions "crocus, iris, squills, asphodels, cyclamen, and others."

Feniuk and Kazantzera (1937) report that *Dipus sagitta* plugs its burrows in hot weather to exclude heat, but does not plug them in cold weather, or only to a slight extent. The animals emerge from their burrows later in the evening in hotter weather. The authors say (p. 424):

Of equal importance to the jerboas are the details of their behavior that can be considered as adaptations to life in a desert. The nocturnal and fossorial habits, their action in plugging the mouths of their burrows during the day, thus isolating themselves from the diurnal conditions of the surface, and their manner of placing their nests in a wet stratum of sand,<sup>4</sup> allow them to avoid in large measure the desiccating effect of overdryness of the desert air, as well as the high daytime temperatures. As has been established already . . . the practical dwelling conditions of a good many desert animals differ sharply from the general climatic conditions of a particular district.

While we cannot deny that this may be the true picture for Palestine, we believe the generalization concerning bulbs cannot be extended to cover our area, as Bailey (1923) and Howell (1935) have attempted to do.

<sup>4</sup>So far as known to the present author, our kangaroo rats and pocket mice never reach a "wet stratum of sand."

Bailey (*loc. cit.*) makes much of the capture of a single *D. merriami* which "had its pockets filled with the little juicy tubers of a small *Portulaca*," and of a single instance of underground feeding on a tuber of *Talinum*; and of "thousands of little pits dug over the surface of the ground by small rodents [which] show where roots and bulbs or tubers, all more or less juicy, have served as food and drink."

Thus by statement and inference Bailey emphasizes the abundance and use of subsurface bulbs and tubers as an available source of water. He directs most of his arguments against the possibility that even the best adapted of our desert mammals—pocket mice (*Perognathus*) and kangaroo rats (*Dipodomys*)—can really thrive for any length of time without a regular supply of succulent food. Howell follows the abundance-of-bulbs argument, but admits that some pocket mice may thrive without either water or succulent food.

Against the dependence-on-bulbs argument, we have never taken *spectabilis* with bulbs in the pockets (as was *D. merriami* by Bailey *once*), nor do we consider that the bulbs of our lilies are generally available to them. The bulbs of the commonest lilies of this region (*Brodieae*, *Calachortus*, and *Hesperocallis*) lie at depths of from several inches to 1 foot or more. The first two named are generally in rocky soil, sometimes difficult to unearth with a geologist's pick. Those of *Hesperocallis*, a species occurring chiefly in *Dipodomys deserti* territory, may be in soft sand but at a depth of as much as 2 feet. No indication of rodents excavating these bulbs has been seen.

*Portulaca* tubers are too large to be pocketed by *D. merriami* or even *D. spectabilis*, and the finding of bulbs either in the cheek pouches or in the storage chambers is a rare exception. The "thousands of little pits" are still something of a mystery to us, and we know of no tiny bulbs to fit them nor of any lying so shallow. Some of these pits may be accounted for by the heavy beaks of our thrashers which we have seen doing similar work.

Both Bailey and Howell reported that *Dipodomys* spp. lose condition when kept long in captivity on air-dry food, and to this we agree. But we emphasize that the conditions of life in captivity are almost certainly more arid than those which the animal selects for itself in the natural habitat. Snakes dehydrate rapidly in a laboratory cage and drink water avidly, or lie in it. The Gila monster (*Heloderma suspectum*) in a laboratory cage spends much of the time lying in the water pan, which it assuredly cannot do in its native haunts.

Many additional records and observations bear on this problem. For example, in our laboratory a tiny pocket mouse (*Perognathus apache*) lived in a small cage from May to November on air-dry rolled oats, without green food or water. It had a small nest for retreat and was in a basement room during the hot months. Even so, it is doubtful that conditions for retention of moisture were as good as in its natural habitat. Although the little animal by

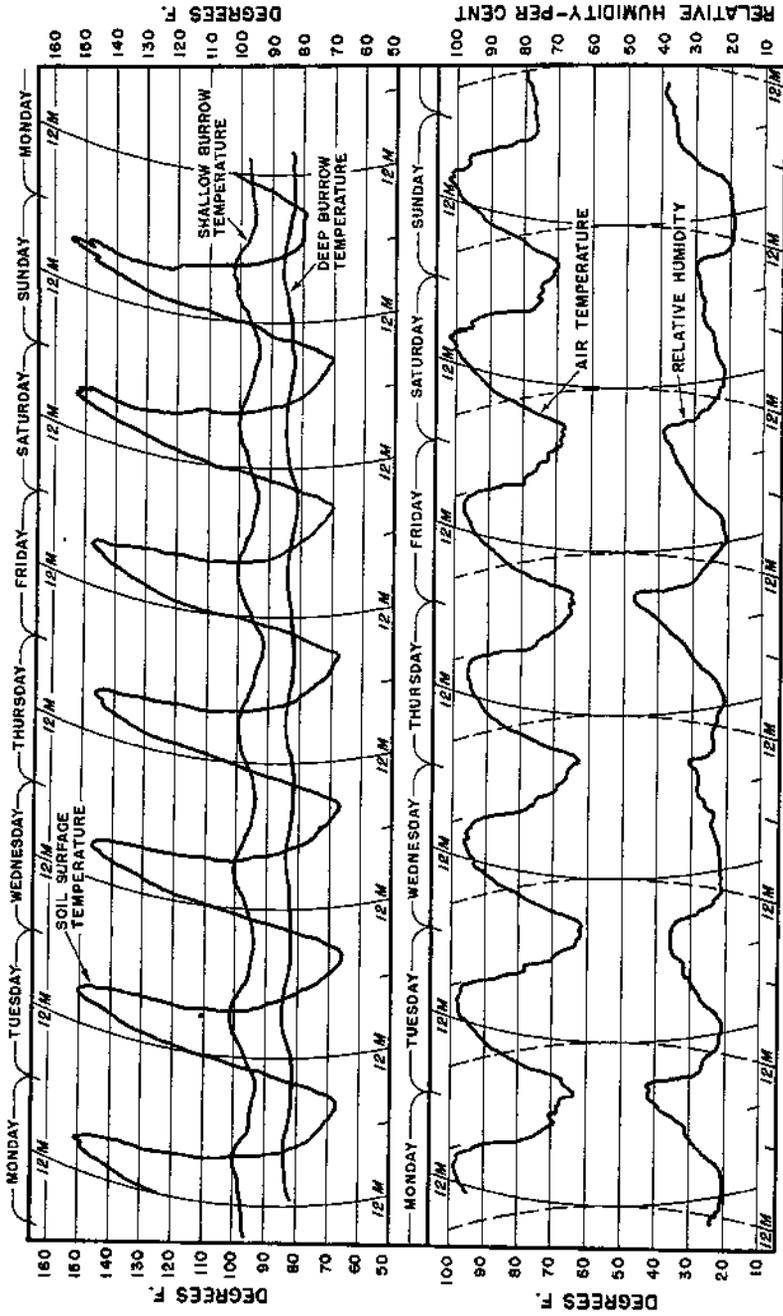


Figure 1.—The microclimate of *Dipodomys spectabilis* for one week.

November was in a weakened condition, it surely demonstrated a remarkable ability to exist without free water or succulence. Stephens (1906, p. 171) says of a captive *Perognathus fallax*:

It would eat no green plants or roots that I gave it and would not touch water. During the last three years of its life I gave it only dry barley or dry wheat and no water. It is a mystery to me how such an animal can live for years and thrive on dry grain without water or moisture in any form, but this one certainly did.

(This was, presumably, in San Diego, with a more humid atmosphere than that of Arizona.) Howell (1935) reports a similar record for the same species.

Hall and Linsdale (1939) discussing *Microdipodops megacephalus*, say (p. 302):

To judge from the arid character of places where specimens have been taken, it seems improbable that the kangaroo mice need a regularly available supply of water. Furthermore, the individual kept in captivity for six months was given no water or even succulent food.

Hawbecker (1940, p. 393) records an observation on *Dipodomys venustus* as follows:

A captive animal kept for five months took any commercial seed (oats, rye, barley or vetch) in preference to green material, such as cabbage, lettuce, grass, or root vegetables. This same animal did not use water put into the cage, but lived for months without using either water or green food material.

We agree with Howell and Gersh (1935, p. 2) in saying "Some of the Heteromyidae are probably able to withstand a greater degree of desiccation than any other animal, but within the family there is much variation in this ability."

The author's first experiences with *spectabilis*, when he was new to the country and trying to trap whatever animal lived in those conspicuous mounds, bear out all cage feedings and storage examinations. Traps were baited with succulent bits of sweet potato, carrot, turnip, and apple, but not one *Dipodomys* was taken with those baits nor a bait destroyed. The animal is easily trapped with dry oatmeal bait.

One of the most remarkable habits connected with the dry-food storage of kangaroo rats was discovered by Shaw (1934). He found that the giant kangaroo rat, *Dipodomys ingens*, uses an extensive series of small surface pits in the neighborhood of its den for the purpose of drying collected food materials preparatory to storing. Could anything better illustrate its preference for dry food?

Vorhies and Taylor (1922) showed (pp. 18-28) that the stored foods of the banner-tailed kangaroo rat, *Dipodomys spectabilis*, are almost exclusively air-dry materials, although some succulent food is eaten at special seasons. No effort was made, nor does it seem feasible, to determine the precise proportions of succulent and air-dry foods used. Discussing this the authors say (p. 25):

At times, more especially in the seasons of active growth, some of the green and succulent portions of plants are eaten. This was very noticeable in the spring of 1919, when a most luxuriant growth of Mexican poppy

(*Eschscholtzia mexicana*) occurred. Stomachs at this time were filled with the yellow and green mixture undoubtedly produced by the grinding up of the buds and flowers of this plant. Small caches of about a tablespoonful of these buds were also found in the burrows at this time. Occasionally in spring one may find a few green leaves of various plants, *Gaertneria* very commonly, tucked away in small pockets along the underground tunnels, indicating that such materials are used to some extent. As has been shown in detail, however (Table 1), the chief storage, and undoubtedly the chief food, consists of air-dry seeds.

The character of the storage, the absence of rain for months at a time in some years, and the consequent failure of green succulents show that without doubt *spectabilis* possesses remarkable power, as to its water requirements, of existing largely if not wholly upon the water derived from air-dry starchy foods, i.e., metabolic water serves it in lieu of drink (Nelson, 1918, p. 400), this being formed in considerable quantities by oxidation of carbohydrates and fats (Babcock, 1912, pp. 159, 170). During the long dry periods characteristic of southern Arizona, no evidence that the animal seeks a supply of succulent food, as cactus, is found; and if it may go for two, three, or six months without water or succulent food, it is reasonable to suppose that it may do so indefinitely. In the laboratory *spectabilis* ordinarily does not drink, but rather shows a dislike for getting its nose wet.

*D. spectabilis* (Pl. I 2) inhabits a labyrinthine underground den (*loc. cit.*, Fig. 2) in which the nest is usually at the end of a blind tunnel at an average depth of nearly 2 feet. Although most of the several den entrances remain open by day, it is unlikely that there is much circulation of air through such a maze of passages.

We may now examine the records of the climatic conditions in which *spectabilis* actually lives, remembering that it is quite strictly nocturnal in habit. Figure 1 is a composite of the records from three soil thermographs (upper portion) and a hygrothermograph (lower portion), placed as described under "Methods" (p. 490). This is for the week ending June 22, 1931, which is near the end of the usual hot, dry, "arid fore-summer." Particularly striking is the extreme daily range of temperature (about 80 degrees F.) that this small animal would have to endure if it chose to remain in its bare front dooryard by day, as shown by the "soil surface temperature" tracing. The mean maximum in midafternoon is about 150 degrees F.<sup>5</sup> A few feet above ground, and in shade, a daily fluctuation of only 40 degrees (air temperature) is to be endured. No small mammal of this area lives in a comparable situation, save temporarily, but many birds endure approximately this climate. At arm's length, about 18 inches, within an open-mouth burrow (shallow burrow temperature) the daily range is less than 10 degrees, the maxima fluctuating somewhat above and below the air temperature maxima. There is no evidence that any of our small mammals frequent this rather uncomfortable zone; though some of the smaller pocket mice with shallower burrows may experience it more than others. The "deep burrow" temperature record clearly indicates a relatively comfortable home for the kangaroo rat, with the temperature nearly static at a little above 80 degrees. It is noteworthy, now

<sup>5</sup>All temperatures in this paper are in degrees Fahrenheit.

TABLE 1.—MAXIMUM TEMPERATURES AND TEMPERATURE RANGES WITHIN AND OUTSIDE A DEN OF THE BANNER-TAILED KANGAROO RAT, IN DEGREES FAHRENHEIT (1930-31)

Week ending	Air		Soil surface		Entrance tunnel		Deep burrow		Precipitation
	Max-imum	Daily range	Max-imum	Daily range	Max-imum	Weekly range	Max-imum	Weekly range	
Oct. 20	93	42	125	82	78	12	74	4	None
Nov. 17	76	30	105	69	74	5*	73	4	None
Dec. 22	66	33	83	42	53	13	54	6	None
Jan. 19	68	36	85	38	53	14	48	3	None
Feb. 9	77	34	101	62	58	12	56	3	.16 inch
March 16	79	32	114	60	61	12	---	—	None
April 13	87	33	132	92	72	8	---	—	None
May 18	95	36	145	86	81	9	76	4	None
June 22	103	39	155	85	92	9	86	5	None
July 13	103	33	155	81	91	11	88	6	.13 inch
Aug. 24	101	34	147	78	84	12	83	5	.91 inch
Sept. 14	96	31	143	75	80	10	78	4	.92 inch
Average		34		71		10.5		4.4	

\*Burrow opening closed.

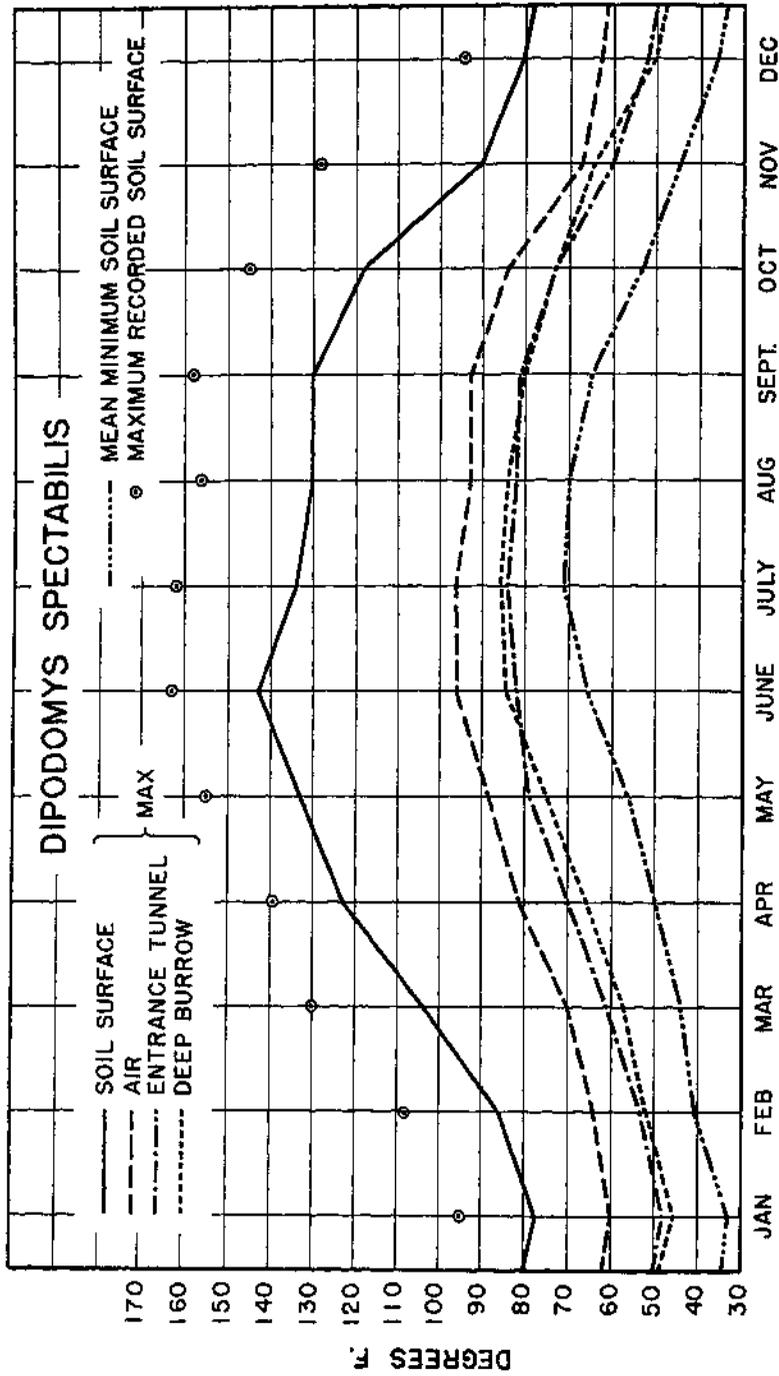


Figure 2.—The microclimate of *Dipodomys spectabilis* for twelve months.

that we have air-cooling by evaporative coolers in so many homes in southern Arizona, that temperatures of from 80 to 84 degrees in the house, when the temperatures outside run from 100 to 105 degrees, are found to be very comfortable.

The year-round temperature environment of *D. spectabilis* is shown in Figure 2. Here are plotted the mean maxima each month for the different locations within and without the den; the maximum soil surface temperature reached each month during the whole period of recording on this species; and the mean minimum soil surface temperatures. All means are calculated from the records of the period of recording rather than of any single year.

The mean minimum air temperatures are not shown on the graph, because they are so close to the mean minimum soil surface temperatures for the entire year. The air minima and the soil surface minima are no more than 3 degrees apart any month, and in some months they are identical. In winter the air temperature usually falls a little below the soil surface temperature at night because of the heat-holding capacity of the soil. Wet soil on a clear summer night may cool below the air minimum by radiation and evaporation. The daily range of air temperature throughout the year averages from 25 to 30 degrees; and of soil surface temperature from 40 to 75, with an occasional extreme of 80 between day and night. At arm's length in the burrow the daily fluctuation for a week is no more than 5 degrees.

In Table 1 are shown for one week of each month for a full year the maxima of the various recordings and the corresponding temperature ranges. The daily range is given for the more extreme changes of air temperature and soil surface temperature, while for the relatively stable entrance tunnel (arm's length) and deep burrow the weekly ranges are given. Note the extreme daily range of 92 degrees in soil surface temperature the week of April 13, 1931. This is an extremely severe range of temperature for an animal to endure. None endures it so far as we have been able to observe.

Thus, it is evident that by remaining within this shelter by day the kangaroo rat avoids great extremes of heat. Even if safely perched in a bush above the soil surface, it would be subjected to a high air temperature and low humidity, as well as to the further desiccating effect of the wind.

Not only is the deep burrow temperature much more favorable to retention of moisture in the body, but the humidity must be comparatively favorable. Unfortunately there did not exist, so far as known to this writer, any apparatus with which relative humidity within the narrow confines of these burrows could be recorded. It was not even feasible to secure reliable single readings of humidity. Certainly the psychrometer cannot be used, and other types, even the duff hygrometer, are soon rendered useless by dirt and gravel. A few unsatisfactory readings were taken. These indicated, as would be anticipated, that humidity is at least a little higher within the burrow than outside at the driest period, and must be considerably higher when the soil is quite moist. In

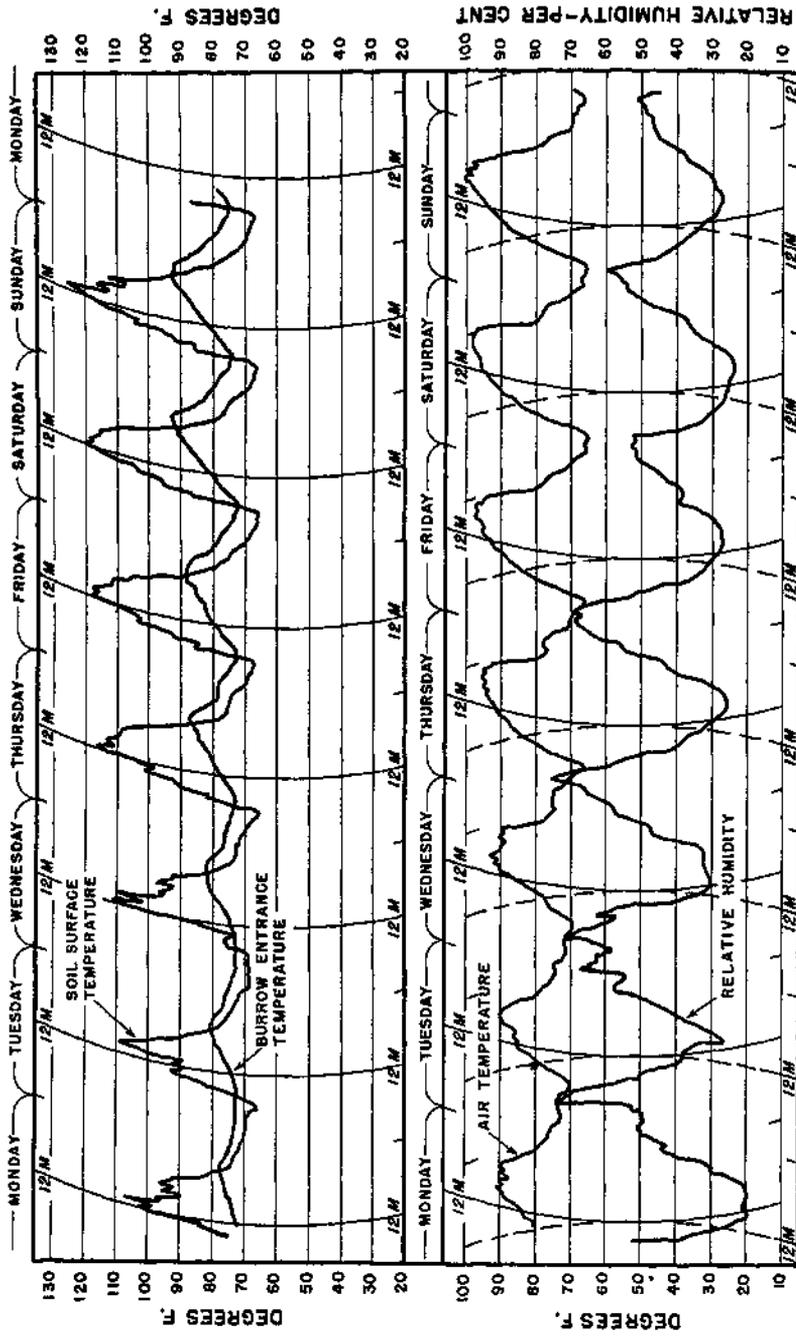


Figure 3.—The microclimate of *Nectoma albigua* for one week.

the nest and blind tunnel, even if the humidity be not high when the inhabitant is out, it must build up with the animal present to a point well above that outside. The animal must respire, though it does not perspire.

Free water for drinking is unavailable in the typical *spectabilis* habitat save when it rains, and there is good evidence that these animals usually remain in their burrows on wet nights (Vorhies and Taylor, 1922). Weeks or even months may elapse without rain, particularly in the extreme southwestern corner of Arizona where *Dipodomys deserti* manages an existence under still less favorable moisture conditions than those common to *spectabilis*. Dew occurs as a rule only for a night or two immediately following the heavier rains. Any species of a low radius of mobility surviving in such an environment must be able to get along indefinitely without free water. A recent writer in *Natural History* suggests absorption of water through the skin. Not the slightest evidence for this is known to this author.

Apparently we have here a significant correlation between ability to live without free water on a diet low in water content, and a water-conserving habit (nocturnal) and habitat (deep burrow). This appears to the author to explain the phenomenon of life in an arid environment without drinking water. The animal conserves by its mode of life every possible bit of water, including not only that contained in its food, but also that which is the product of metabolism, "metabolic water." In our usual thinking we consider metabolic water, since it is a by-product of the metabolism of carbohydrates, as "waste"; but it is certainly H<sub>2</sub>O, and just as good as any other water. It is waste only if the animal can afford to waste it.

Since publication of our bulletin on the kangaroo rat (Vorhies and Taylor, 1922), the present author has come gradually, and independently, to the conclusion (already published by Howell and Gersh, 1935) that metabolic water is only a by-product of everyday metabolism; that it is not produced in increased quantities by xerophilous animals; and that it is not necessary to invoke the presence of a special physiological "factory" for its production.

Howell and Gersh (*loc. cit.*) by physiological experimentation disclosed an important additional adaptation to scanty water supply in the ability of the kangaroo rat (*Dipodomys*) to resorb water from within the kidneys and from the bladder. Furthermore, this resorption was found to be greater in amount, both in kidneys and bladder, in "dehydrated *Dipodomys*" (fed on dry foods) than in "wet-fed" individuals of the same species.

#### THE WHITE-THROATED WOOD RAT

We may next examine the data on the habitat and foods of the white-throated wood rat, *Neotoma albigula* (Pl. II 2), another dweller in the arid regions. This species is found chiefly, though not exclusively, in the Lower Sonoran Zone. In the least favorable habitat of this zone, creosote bush (*Larrea*) without cactus,

*Neotoma* is not common but can exist there. It is much more abundant at slightly higher levels, or where more cactus and mesquite or other desert succulence is present.

The *Neotoma* habitation is not strictly a burrow, but rather a sort of half-basement apartment sunk below the level of the soil and heavily roofed (and shaded) by a pile of debris, commonly called a "pack rat's nest" (Pl. II 1). The actual nest, however, lies hidden in the basement, sometimes beneath the earth, but often with no roof other than the pile of litter. Here we have an animal which is less well protected from heat and humidity than the kangaroo rat. In no typical case is the protection from high temperature and low humidity so complete as in the kangaroo rat burrow. In Figure 4 are shown essentially the same data on the wood rat as presented in Figure 2 for the kangaroo rat.

Perhaps the most noticeable contrast with the *spectabilis* graph is the much lower soil surface mean maximum. This is probably of little actual significance in the life of the animal, since this species also is chiefly nocturnal (slightly crepuscular) and is, therefore, not called upon to endure even these maxima. The difference is due to the fact that the soil surface about the *Neotoma* den is seldom entirely bare—in this case a sparse ground cover of grass, weeds, and *Haplopappus* gave an astonishing amount of protection from heating up of the soil. The air maximum curve, though it differs month by month from that of *Dipodomys*, is likewise not significant, since it is not a difference of habitation but of different years at essentially the same location. The two locations were but 100 yards apart. Calculation of the mean for the whole period covered at both locations shows only 1 degree of difference.

In the "nest" maxima a possibly significant difference may be noted. *Neotoma* in the critical (dry) month of June endures a mean maximum of 88 degrees as compared with 84 for *D. spectabilis*. This is not a great difference, but at least the kangaroo rat has the better of it for conservation of water. Though without experimental proof, there can be scarcely a doubt that *Neotoma* is much more exposed to water loss by evaporation. Its nest is much less well protected from air currents than that of *Dipodomys* and must be less humid, being so near the soil surface that the surrounding soil is quite dry in the hottest, driest seasons. The animal is often active early in the evening, three to five hours earlier than the kangaroo rat, and not infrequently is seen by full daylight. In brief, it does not seem to be so good a water conservationist as its neighbor.

The food of *Neotoma albigula albigula* has been exhaustively studied by Vorhies and Taylor (1940). Our food data on the wood rat are more complete and satisfactory than on the kangaroo rat, owing mainly to the fact that we had a series of stomach analyses to supplement the field observations on storage, and much ocular evidence of attacks on plants. This rodent neither stores nor consumes any considerable quantity of seeds primarily for the seeds, with the possible exception of mesquite; and in this case we do

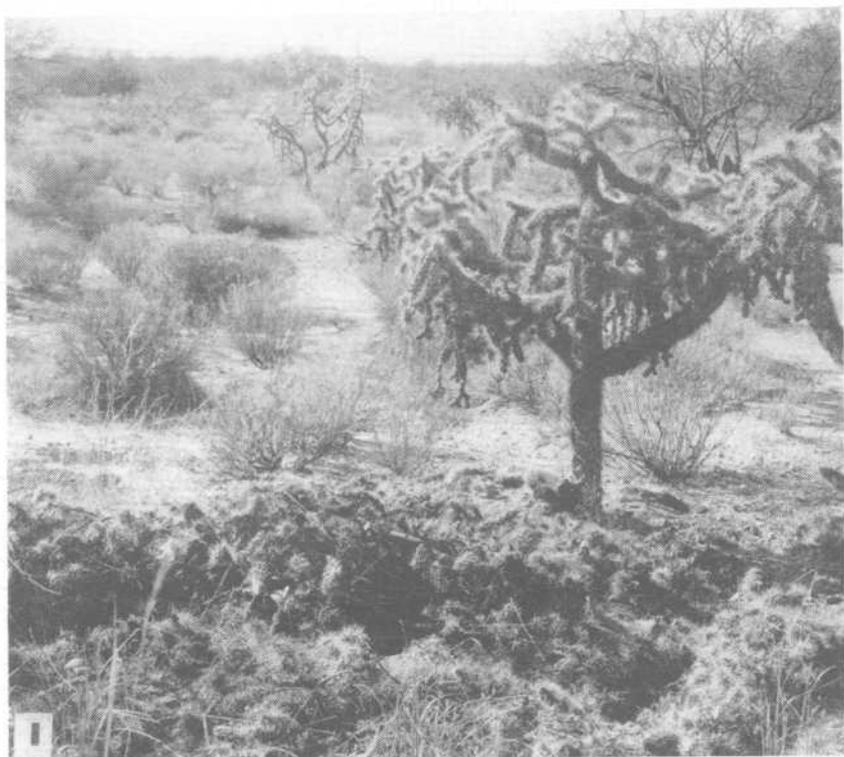


Plate II.—White-throated wood rat and habitation: 1, "Pack-rat den" of *albigula*. 2, *Neotoma albigula* in its shelter after the "lid is off."

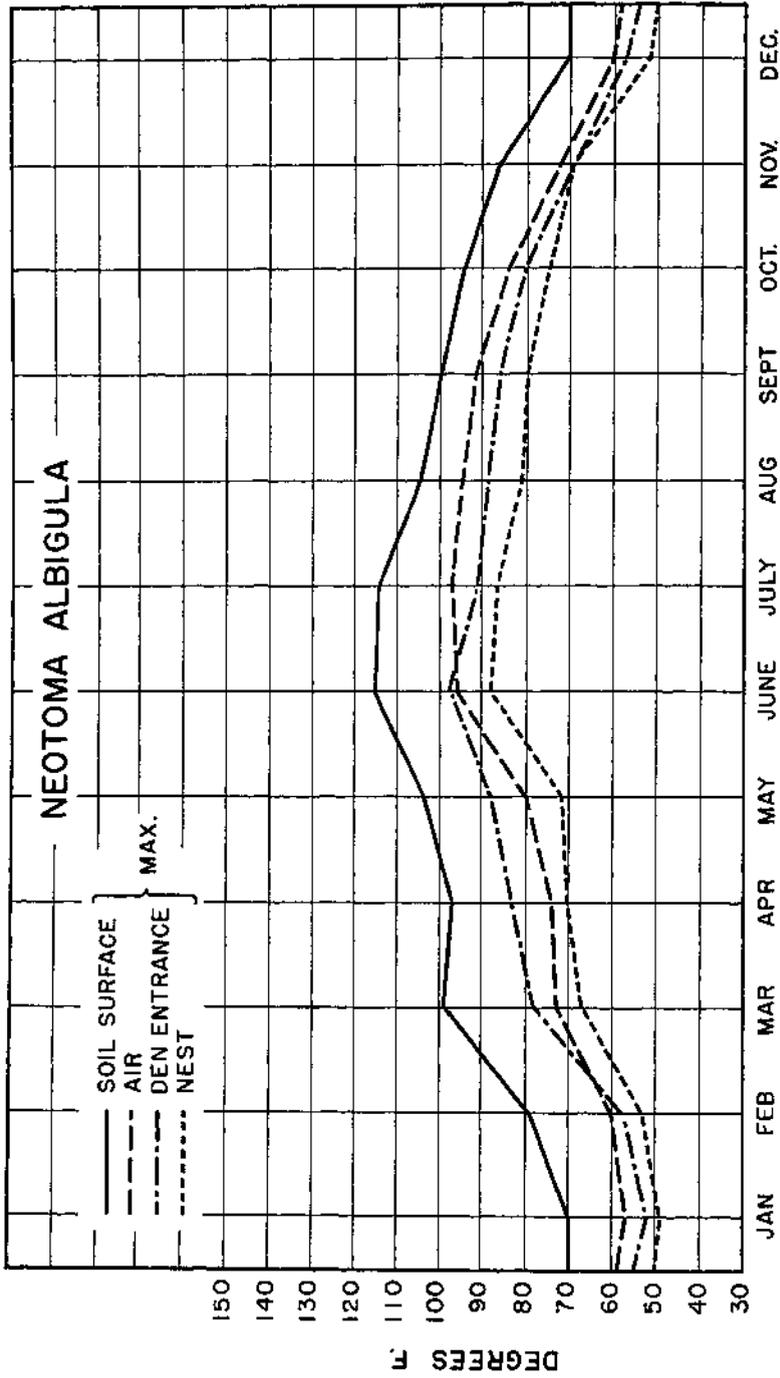


Figure 4.—The microclimate of *Neotoma albigula* for twelve months.

not know whether the seeds themselves or the sweet, nutritious pods are the more desired item. Probably the latter. This is not highly important to our comparisons, however, since highly succulent cactus (nearly 90 per cent water), constitutes 43.8 per cent of all foods for the year. Cactus fruits are stored and eaten, but the seeds appear to be discarded wholly or in large part. Mesquite constitutes 30.2 per cent of the annual food, but we know that a part of this is green leaves. It is further significant that the greatest consumption of cactus occurs in May, one of the driest months of the year, when it amounts to more than 90 per cent of all food by bulk. In June, an equally severe month, cactus decreases in quantity, but in favor of mesquite, which is then green and growing and the pods not yet dry. This animal uses a much moister diet than that of the kangaroo rat. At all seasons wood rat attacks on prickly pear plants are conspicuous, and on the cholla type cacti are common enough. These attacks are not confined to, but are intensified by, drought periods. *Neotoma* uses but little air-dry food.

A series of records was taken in and outside a wood rat den, including one soil thermograph record in the opening of the den, and one with the sensitive bulb inserted beneath the "brush pile" in the approximate location of the nest. An "arm's length in burrow" record is inconvenient (to say the least) on account of the cactus. From these records for the week of June 19-26, 1932 (Fig. 3), we see that *Neotoma*, also a nocturnal rodent, has to endure maxima above 90 degrees not infrequently, and it is reasonably certain that the humidity is little, if any, higher than in the open, since wind can certainly cause a circulation of air through practically the entire structure, and the depth is shallow.

This desert-adapted rodent depends not so much on *conserving* its precious water as on securing a sufficient supply with its food. The wood rat is quite as independent of free water for drinking as is the kangaroo rat, but meets the problem in a different manner.

*Neotoma albigula*, the white-throated wood rat, is shown to be somewhat less well protected in its home den from extremes of heat and humidity than *Dipodomys spectabilis*. The difference, so far as indicated by the temperature records, is not so great as observation might lead one to believe. It is to be regretted, since the locations were practically one, that parallel records for the two species were not kept over the same years, thus eliminating any seasonal differences. Weather bureau records for the respective years show generally normal temperatures for the hot months of 1930, 1931, and 1932, but above normal for 1933. Thus, June of the latter year is recorded as 3.4 degrees above normal and "second warmest in 20 years"; July, 2.4 degrees above normal and "warmest in 32 years"; August, 1.5 degrees above normal and "mean temperature for the month was highest since 1910." It is believed that the observed habit differences between the distinctly nocturnal kangaroo rat and the definite tendency to crepuscular and even occasionally diurnal habits of the wood rat increase the

water loss of the latter more than the temperature records alone indicate. Although we have no data on the relative dryness of the respective types of dens, the *Neotoma* den must be the drier in critical times.

The food of *Neotoma albigula* on the Santa Rita Experimental Range is overwhelmingly succulent, rather than dry. At no time of year does the wood rat neglect the use of food relatively high in water content. There is little or no evidence of dry seeds being used. Mesquite beans are stored but are used apparently for the pods, which are high in carbohydrates; and these stores so often remain largely uneaten as to convict the wood rat of being a hoarder.

Vorhies and Taylor report (1940, p. 496 *et seq.*):

Cactus is the leading food through much of the year, constituting 43.80 per cent of all food taken. For 6 months of the year this food exceeds any other in quantity consumed (January, March, April, May, June, November). It is exceeded by mesquite in February, July, August, October, and December, and by herbs and shrubby vegetation in September. Mesquite constitutes 30.2 per cent of the annual total of food.

There is a tendency for mesquite and cactus to be complementary in the wood rat's diet.

When either shows an increase, the other decreases.

Like other desert rodents, *Neotoma* has no need for a supply of drinking water. Nor is its adaptation to the aridity of its environment so difficult to explain as is that of kangaroo rats and pocket mice. Living in shallower burrows than *Dipodomys*, *Neotoma* is less well protected from heat and dryness, and doubtless requires more water from some source. That its food is the source of its water supply seems so evident as to require little discussion. Taylor, observing caged wood rats, kept water in the cage but never saw the animals drink or any evidence of drinking.

Its principal foods are succulent and furnish a supply of water which is actually abundant as compared with that available to *Dipodomys* and *Perognathus* in their relatively dry foods. Cactus, which is nearly 90 per cent water, makes up 43.8 per cent of the food for the year. Mesquite is the next largest food item, but varies in succulence according to season and parts eaten. The fresh pods and green leaves are succulent, while the ripe pods are quite dry. The pods are very sweet, however, and the utilization of carbohydrates yields water as a by-product. The grasses, furnishing less than 5 per cent of the annual food, are taken chiefly at the season when green and succulent, as are also the forbs. Insects, although a decidedly minor item in the total volume of food, are juicy morsels.

The variations in quantity of the two most important and complementary items in the diet of the wood rat (cactus and mesquite) show some indication of the greater use of cactus in the drier seasons. In May, for example, one of the driest months of the year, cactus made up over 90 per cent of all food by volume. Grass increased in August and reached its maximum use in September, precisely when there is the greatest abundance of green grass and the weather is becoming dry.

## THE GROUND SQUIRRELS

The round-tailed ground squirrel, *Citellus tereticaudus*, is a small rodent of the arid Southwest. It is almost unique in its strictly diurnal habit, which may mean exposure to high temperature and low humidity; which in turn must mean increased water loss. The only other small diurnal rodents of the hot Lower

Sonoran Zone of Arizona are other species of the same genus, including *Citellus (Amмосpermophilus) harrisi*. So far as we have observed there is little, if any, essential difference in the temperature and humidity conditions to which these several species and subspecies have become adapted, nor in the character of the adaptations. (Some live in the cooler climate of the higher altitudes.)

The climatic picture for *C. tereticaudus* in hot weather is shown in Figures 5 and 6. Here (Fig. 5) are the soil surface and deep burrow temperatures as recorded during the week ending June 8, 1936 (above); and the air temperature and relative humidity for the same period (below).

Extremely high temperatures are reached on the ground surface at about 2 to 4 P.M., the mean maximum for this week being 156 degrees, in contrast to a mean minimum of 55. The maxima here are much higher than in the dooryard of *Neotoma*, owing, as in the case of *Dipodomys*, to the characteristic bareness of ground. At most, only extremely short vegetation, affording no shade, is present. Meantime the air temperature well above the ground reaches a mean maximum of 94 degrees, with relative humidity ranging down at the same time to a mean (for this week) of 29 per cent.

These extremes would necessarily cause considerable water loss if they were actually endured. But it will be noticed that both high temperature and low relative humidity exist for only a few of even the daylight hours. This is particularly true of the extremes of the ground surface. As a matter of fact, these rodents meet the situation by: (a) restricted time of activity; (b) spending some of their active time off the ground or in the shade; (c) remaining part time within the much cooler burrow; (d) entering into an estivation-hibernation period which includes the dry, warm, late summertime; and (e) use of succulent foods.

The times of greatest activity are during forenoon and afternoon, before and after the hours of greatest extremes of heat and low humidity. The time of activity is so variable, depending apparently upon the heat of the day, that precise statements of time cannot be made by clock hours. *C. tereticaudus* does not, however, work in the very pleasant morning hours, seldom appearing before 8 A.M., even when the weather has become quite warm and the days long. Soon after this hour, in quite warm weather, activity is at its height and may continue until noon or after. The hotter the weather, however, the earlier the animals retire to their burrows. They remain within until a late afternoon hour, when they resume activity which continues until evening, relatively nearer to sundown than is the beginning of morning activity to sunrise. There are individual exceptions even to this general statement, there being scarcely an hour of the day when, in the course of long observation, some individual has not been seen.

When actively feeding, the animals may avoid the high soil surface temperature by climbing into a bush or shrub from 1 to

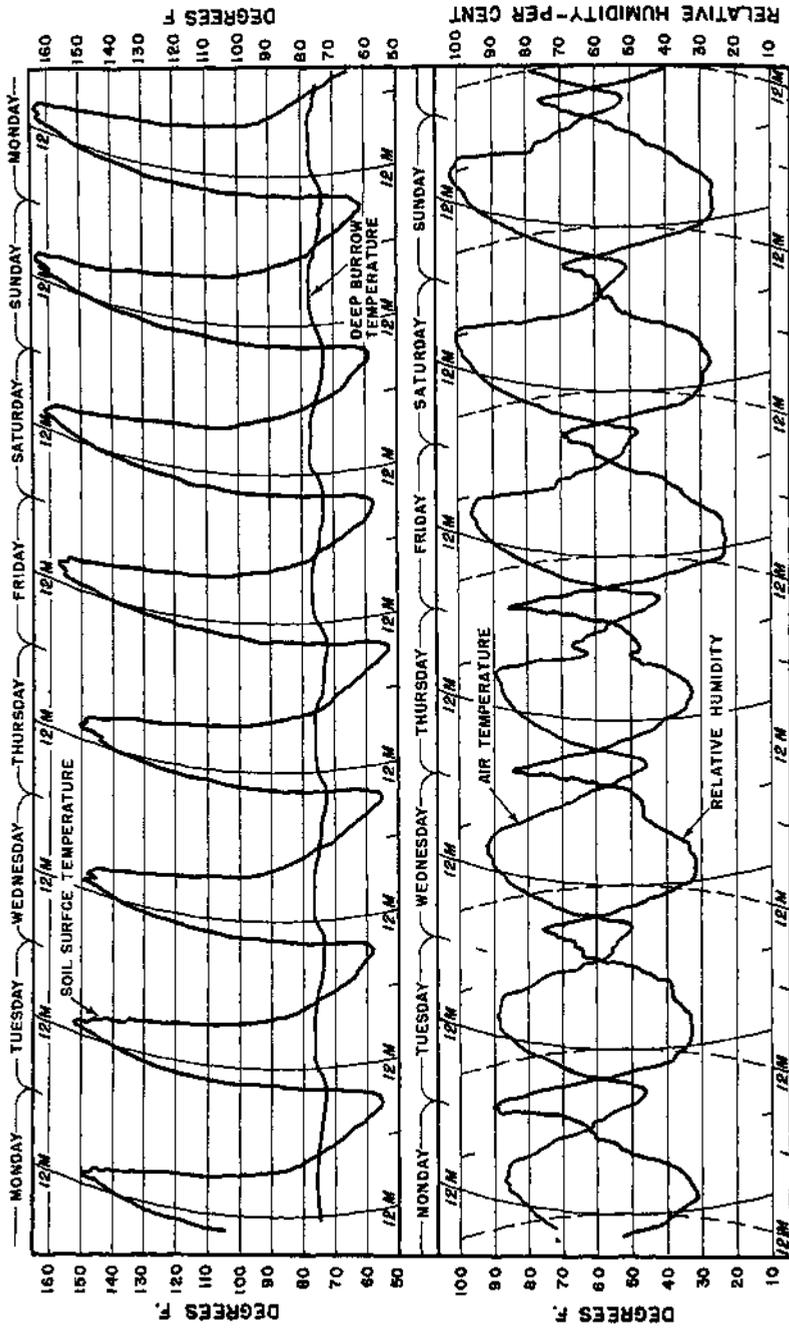


Figure 5.—The microclimate of *Citellus tereticaudus* for one week.

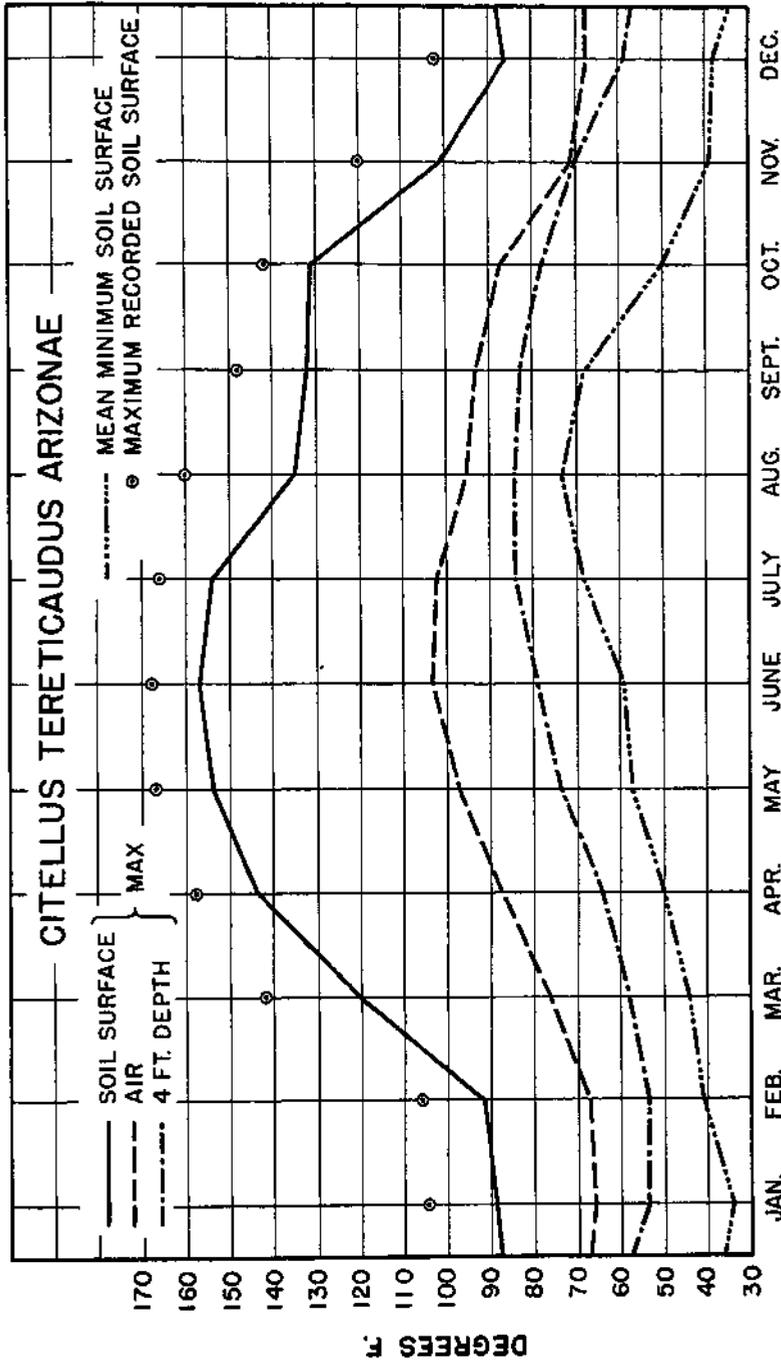


Figure 6.—The microclimate of *Citellus tereticaudus* for twelve months.

4 feet above ground; by seeking the partial shade of a small plant; or by temporary retreat into the protection of the burrow. Ascending a shrub does not appear to be primarily for the purpose of cooling the feet, since it is a part of normal feeding activity, but it cannot be doubted that it is a relief from the ground temperature.

(Individual ants have been observed, when ground temperature was high and most of the colony inactive, to run rapidly across a few inches of bare ground, climb a 4-5-inch-high sprig of vegetation, remain a half minute, and resume their journey. It looked like an escape from too great heat.)

When the situation becomes too uncomfortable, the whole colony disappears into the burrows, there to remain with such exceptions as have already been noted. The deep burrow temperature is that of an average comfortable, evaporation-cooled, modern house, with a range of only 5 degrees for the week charted in which the mean maximum is 77 degrees and the mean minimum 72 degrees. The range may be even less than this in a normal burrow.

It will not be attempted here to explain the curious habit, shared by *tereticaudus* with various other species of the genus *Citellus*, of early fall or late summer estivation which merges into hibernation. Suffice it for our discussion to point out that *C. tereticaudus* disappears in late August and early September, and thus avoids completely the dry, hot autumn period. During this period temperature and humidity are comparable to those of May, and the summer vegetation is drying up. Although thus avoiding one unfavorable period, the animal is active through the hotter, drier, and more critical arid foresummer, May and June (Fig. 6).

While detailed food studies of *C. tereticaudus* have not been made, it may be quite definitely stated that there is little or no consumption of dry seeds or other air-dry food. There is no evidence of food storage, so far as known. These animals begin to emerge from hibernation in February and are common in March, at which season there is normally a scanty to abundant growth of succulent winter annuals, including one or two grasses, e.g., *Festuca octoflora*, forbs, and flowers. The squirrels may readily be observed feeding, grazing on the low vegetation of the ground cover and climbing to browse from the available shrubs. The leaf buds of mesquite (*Prosopis velutina*) are favored when they appear in early April. The ubiquitous burrowweed (*Haplopappus tenuisectus*) is used, and the fruits of creosote (*Larrea*) in May, before they attain complete dryness, are gathered by climbing the bushes. (This is the only edible part of that shrub.) Individuals may sometimes be seen running with a great mouthful of fresh green food, which may be taken into the burrow for (presumably) immediate consumption.

This species feeds avidly on the early green vegetation, and produces a litter of young before the maximum of heat and minimum of humidity dry up the annuals. No further breeding occurs. Adults and young eke out the best existence they may on the succulence of available shrubs, forbs, and bits of green at bases

of perennial grasses. No evidence of dependence on cacti, as with *Neotoma*, has been noted. Free water is taken readily when chance offers. Bird baths and other sources of water are freely visited. They keep to their cool burrows more and more as the heat intensifies. Summer rains of July and August normally produce a luxuriant crop of succulent vegetation. On this fare they wax fat, preparatory to the long sleep or inactivity which begins as the rains cease and vegetation becomes drier.

*Citellus tereticaudus* is not adapted to its desert habitat by any unusual ability to conserve water, while living mainly on air-dry foods, nor by exclusively nocturnal activity. It consequently must have more water from some source than *Dipodomys* (or *Dipus*). This it gets from a mainly succulent diet in the more favorable seasons of the year, supplemented by free water when opportunity offers. Water conservation, when necessary, is attained to some extent by temporary retreats to a deep, cool den in the hotter hours; and by a longer retreat during one of the two hot, dry seasons of the year.

In northern and somewhat higher parts of Arizona, where nevertheless semiarid conditions prevail, lives the prairie dog (*Cynomys*), another diurnal rodent with a water problem. The prairie dog (really a ground squirrel) meets its similar water problem in essentially the same way as the round-tailed ground squirrel. That it inhabits a deep burrow (12 to 14 feet) is doubtless of similar significance—a cooler retreat than the wood rat's, even cooler than that of *Dipodomys*.

#### THE JACK RABBITS

Since the jack rabbit never makes use of a burrow, either as a home or as a retreat from the heat of the sun and the aridity of the atmosphere, no special climatic record for the two species occurring in southern Arizona has been attempted. Here is an animal of relatively large size (Pl. III) which lives in the same region with *Dipodomys*, *Neotoma*, and *Citellus tereticaudus*. It is nocturnal and crepuscular, but lacks a basement room in which to pass the heat of the day. Its climatic environment can be understood by examining the soil surface records outside the *Neotoma* den, in the entrance of the *Neotoma* den, and the regular hygromograph records. The effect of only partial and intermittent shading, as shown by the soil surface graph of the *Neotoma* charts (Fig. 3), is surprising when compared with those of *Dipodomys* (Fig. 1) and *Citellus* (Fig. 5). During the hot season the jack rabbit, undisturbed in its form, invariably is found in partial shade (Pl. III 3); and frequently its form is in the shade of the larger and more densely foliated shrubs such as the desert hackberry (*Celtis pallida*), or the trunk of a fair-sized mesquite tree. A jack rabbit, prevented for a half hour by gentle harassment from enjoying protection from the bright sunshine of May or June, becomes evidently uncomfortable and continually seeks even a little shade. If harassment continues, the animal becomes

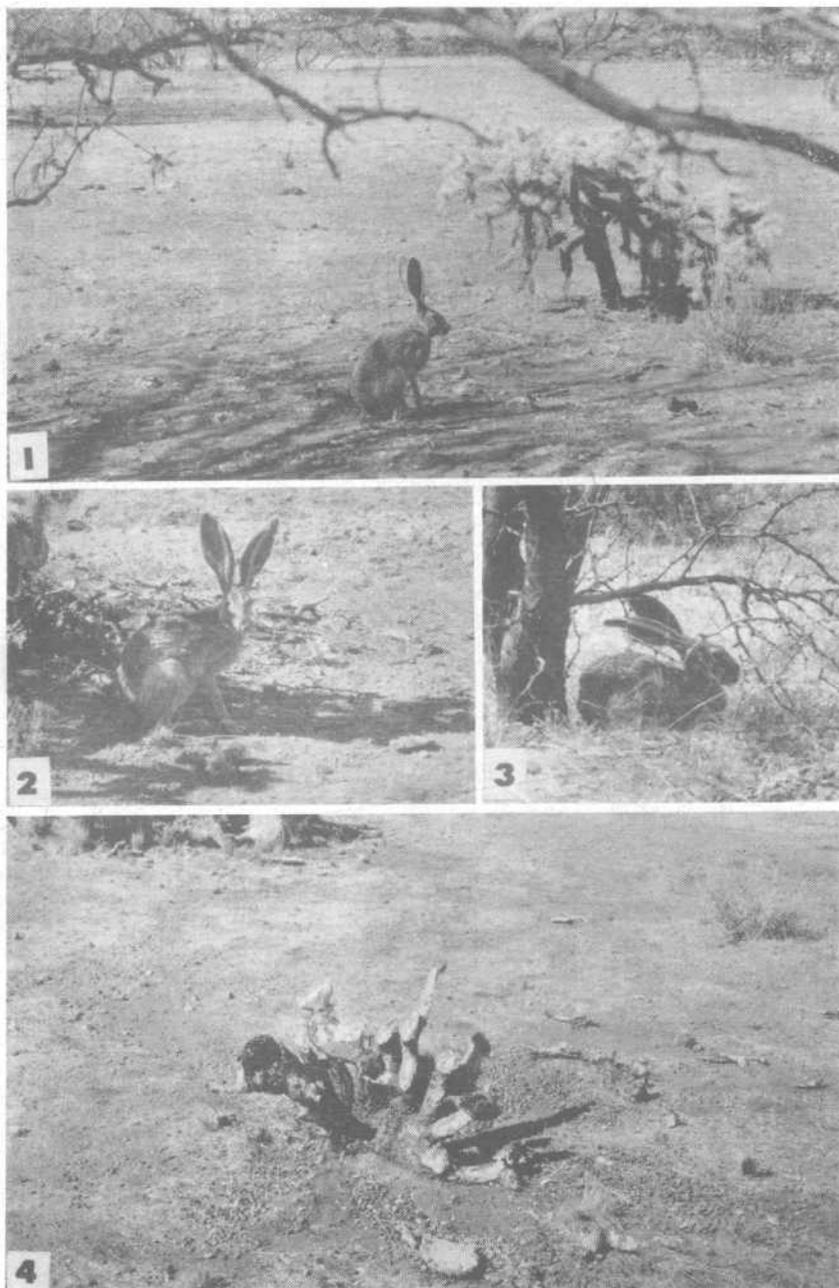


Plate III.—Jack rabbits: 1, 2, 3, *Lepus alleni*, the white-sided or “antelope” jack, seeks even partial shade when the sun is hot. 4, Jack rabbit water supply in drought period—prickly pear destroyed.

more and more uneasy and more persistent in clinging to some shady spot. The location of the form in which the jack rabbit sits by day is so variable in its relation to the amount of shade that it would be practically impossible to choose a typical location for temperature recording. We know the animal does not and cannot endure the temperature of a fully exposed bare surface as recorded in the charts for *Dipodomys* and *Citellus*, but it may sometimes be seen so poorly sheltered (Pl. III I) that the temperature curve would approximate the soil surface record for *Neotoma*. Perhaps more often, in the hottest weather, it finds a heavily shaded spot that would approximate the entrance of the *Neotoma* den. It is our belief, however, that a majority of the forms are so located as to have less than the maximum and more than the minimum protection mentioned. While the ground, in shade, remains a little cooler than the air at maximum, the air 6 inches above the ground is hotter than at the height of the instrument shelter. This would probably mean for the "average" form maximum temperatures somewhat above the air maxima.

In any case, it is certain that the jack rabbit lives in and endures higher temperature and lower humidity than any of the other species discussed. Adding somewhat to its problem is the further factor of more exposure to the desiccating effects of winds.

In view of the above facts and deductions, we may well ask whether the jack rabbit does not require free water. While they do drink in captivity, and probably in the wild when opportunity offers, there is no evidence whatever of their going to and from water holes, tanks, troughs, or other water sources, as would be necessary if free water were a requirement. Animals as large as the jack rabbit could hardly fail to be observed if they moved to and from watering places. Vorhies and Taylor (1933) found the radius of mobility of the jack rabbit to be less in normal times than would be required for trips to water in large areas of southwestern Arizona.

The jack rabbits (*Lepus californicus* and *Lepus alleni*) of the arid regions of the Southwest are unable to conserve water to any such extent as do kangaroo rats and pocket mice. Their water requirements must, therefore, be higher, and if they do not regularly seek drinking water, their needs must be met by the foods consumed.

Vorhies and Taylor (*loc. cit.*) made rather exhaustive studies of the foods of these two species. Figures 2 and 3, pages 524 and 525, give the proportions of the different foods consumed by each species, considered separately—details which need not be repeated here. The important fact in the present connection is that the foods of both, although varying in proportions as between the species, consist entirely of more or less succulent plants. Grass, an important part of the diet, is eaten mainly at those seasons of the year when it is green; mesquite (foliage) of approximately equal succulence, is an even more important item in the diet.

Cactus, very succulent, is less important than one might expect, but is used more in the drier times (p. 529, *et seq.*). Our observations in certain drought years prior to collecting stomachs for food analyses clearly showed the great importance of cactus as a source of water for the jack rabbits (Pl. IV, 4). The authors discuss the seasonal variations in the food of jack rabbits as follows (p. 522):

The food of jack rabbits in the southern Arizona region is intimately related to the alternating dry and rainy seasons (see Table 3, Correlation of Precipitation and Breeding Rate, and Fig. 2). Following the winter rains, when a number of the perennial grasses put forth leaves, the percentage of grass in the diet markedly rises, while the amounts of mesquite and cactus consumed decrease almost to the vanishing point. During May and June, the most arid period of the entire year, the grass dries up, and is much less eaten, while [the now fresh] mesquite maintains a high percentage in the diet and cactus increases. In July and August, following the summer rains, grass becomes by far the most important item in the diet, forming 80 per cent of all food eaten in July and 84 per cent in August. Mesquite falls to its lowest point for the year at this period of maximum grass development, and cactus also decreases. Through the fall months the proportion of grass in the diet declines, while that of mesquite increases, approximately in inverse proportion. While deciduous, the mesquite does not shed its leaves in early autumn; in fact, some leaves remain on individual trees all winter.

Jack rabbits are evidently the least protected from desiccation of the animals discussed, and depend for water more upon succulent foods than any of these, with the possible exception of the wood rat. Exact determination of the relative succulence of the foods of these two is hardly possible, notwithstanding the detailed food studies which have been made.

#### MESQUITE FOREST VERSUS DESERT

Using the equipment described under "Methods" (p. 490), differences in soil surface temperatures, air temperatures, and relative humidity in the shelter of the mesquite forest and outside the forest, on the open mesa or desert were investigated. It is felt that these differences are sufficient to be of ecological significance, though perhaps they are not so directly concerned with the problem of water relations as was anticipated.

The old mesquite forests of the river bottoms of the main water courses of southern Arizona were originally quite dense forests, a somewhat anomalous situation—a forest in the desert. With the growth of towns and cities these forests have gradually disappeared under the woodcutter's ax. Thirty years ago during the fall and winter months long lines of Indian wood wagons creaked their way daily into Tucson bringing the mesquite which was the nearly universal fuel for both heating and cooking. Under this heavy usage the original mesquite forests of the Santa Cruz valley disappeared, and much of even the second growth has been taken out by farm clearing and for fuel. The same thing occurred in the vicinity of Phoenix and Yuma. Along the San Pedro River, with no large towns and less agricultural expansion, much mesquite forest remains, including some remnants of the virgin forest.



Plate IV.—Instrument shelters: 1, In the mesquite forest. 2, On the adjacent mesa "desert." In the background is the edge of the mesquite forest, with additional trees planted about a cottage.

In a dense growth of this mesquite (mostly second growth) were placed the "mesquite forest" instruments (Pl. IV 1). In the thinly vegetated desert or mesa outside the forest duplicate equipment was installed (Pl. IV 2). The difference in elevation of the two sets of instruments was certainly less than 50 feet.

The greatest difference in living conditions between forest and desert is found in the soil surface maximum temperatures (Fig.

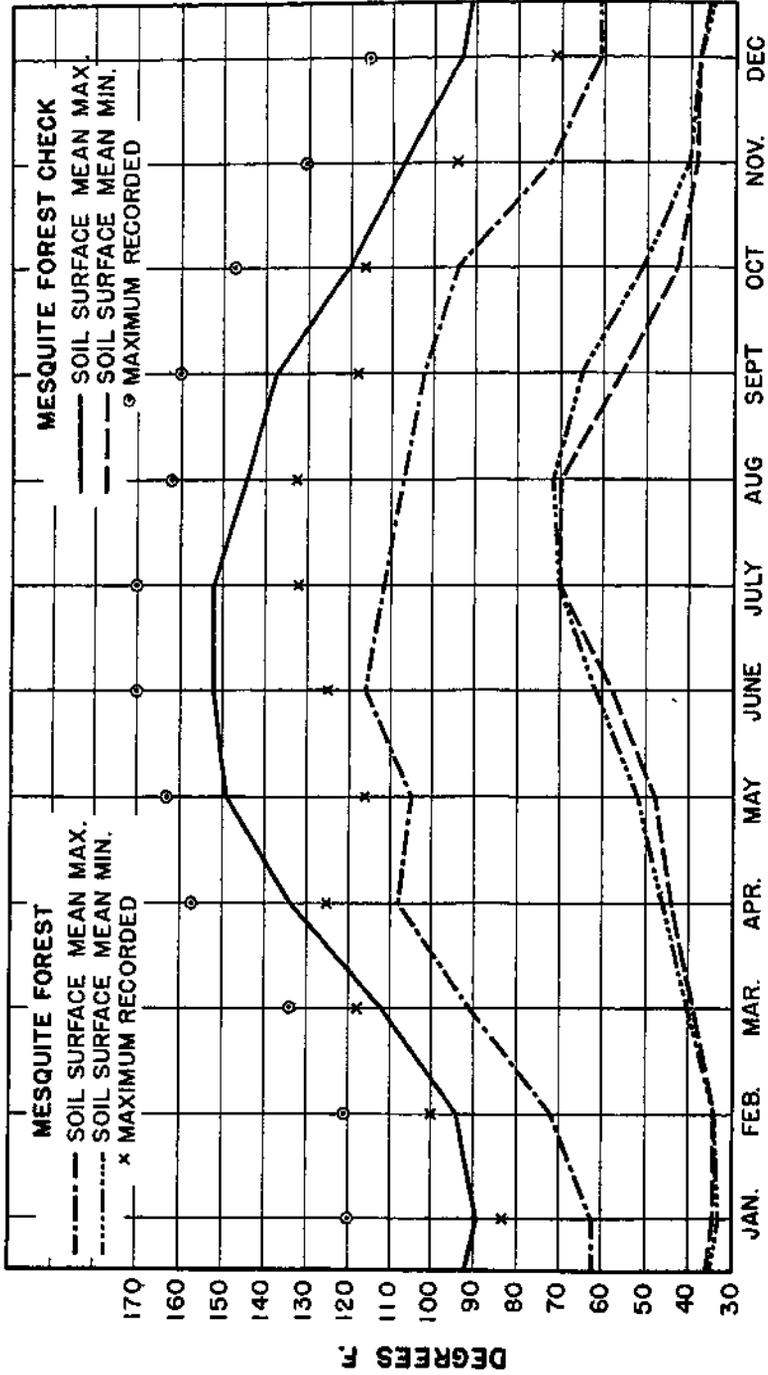


Figure 7.—Soil surface temperatures in mesquite forest, and "check" on adjacent desert.

7).<sup>6</sup> Here the maxima, by the month, as well as the curve of mean maxima are essentially the same as those for *C. tereticaudus*, at near the same altitude and other conditions. In the forest, the effects of shade, of which there is some even when the trees are bare of leaves, are clearly shown by the lower but approximately parallel curve. The irregularity in the latter curve, in May, shows the effect of increased shade resulting from leafing out of the mesquite, which usually begins between April 1 and 15. June, hot and dry, brings a rise in spite of shade, while the rains of July and August exert a decided cooling effect on the soil.

Minima in the forest and outside are not significantly different, but the fact that they are so similar during the hot months may be. The very high daytime temperatures of the exposed soil drop so much more rapidly by radiation at night than does the forest soil as to bring both near the same minima. Therefore, the rodents of the desert (where most of them live) have about as comfortable a substratum for their nocturnal activities as those of the mesquite forest.

There appears to be little significance in such air temperature differences as are found between the mesquite forest and the desert (Fig. 8). No considerable difference should be expected since these are shade temperatures, taken under protection of the instrument shelter. In fact, then, the shade of the forest added to that afforded by the instrument shelter has little additional value. The widest divergence, seen in the July-August maxima, may be due to cooling effects of transpiration and evaporation from soil and foliage following rains (cf. humidity, Fig. 9).

The differences recorded by instruments in this case, however, may not be the whole story. The bodies of the animal inhabitants of these regions may, like our own, register much more discomfort, and doubtless lose more moisture, in the sun of the check area than in the shade of the forest. Herein is the source of the average citizen's dissatisfaction with the officially recorded Weather Bureau temperature compared with his own discomfort while working in the sun.

The records of relative humidity (Fig. 9) show interesting differences and irregularities. It should be emphasized that data on humidity derived from recording instruments are somewhat less accurate than temperature. Temperature can be measured very accurately, and can be automatically recorded with reasonable accuracy by the best instruments. Relative humidity is difficult to determine with anything like equal accuracy, even for individual determinations; while the recording instruments are still less accurate. Further, the relative humidity of the atmosphere seems to be subject to even more fluctuation than air temperature. Notwithstanding these difficulties, it is felt that the overall picture of humidity, as shown by the graphs, is sufficiently accurate to have some significance.

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<sup>6</sup>"Mesquite forest check" = "desert" or "mesa."

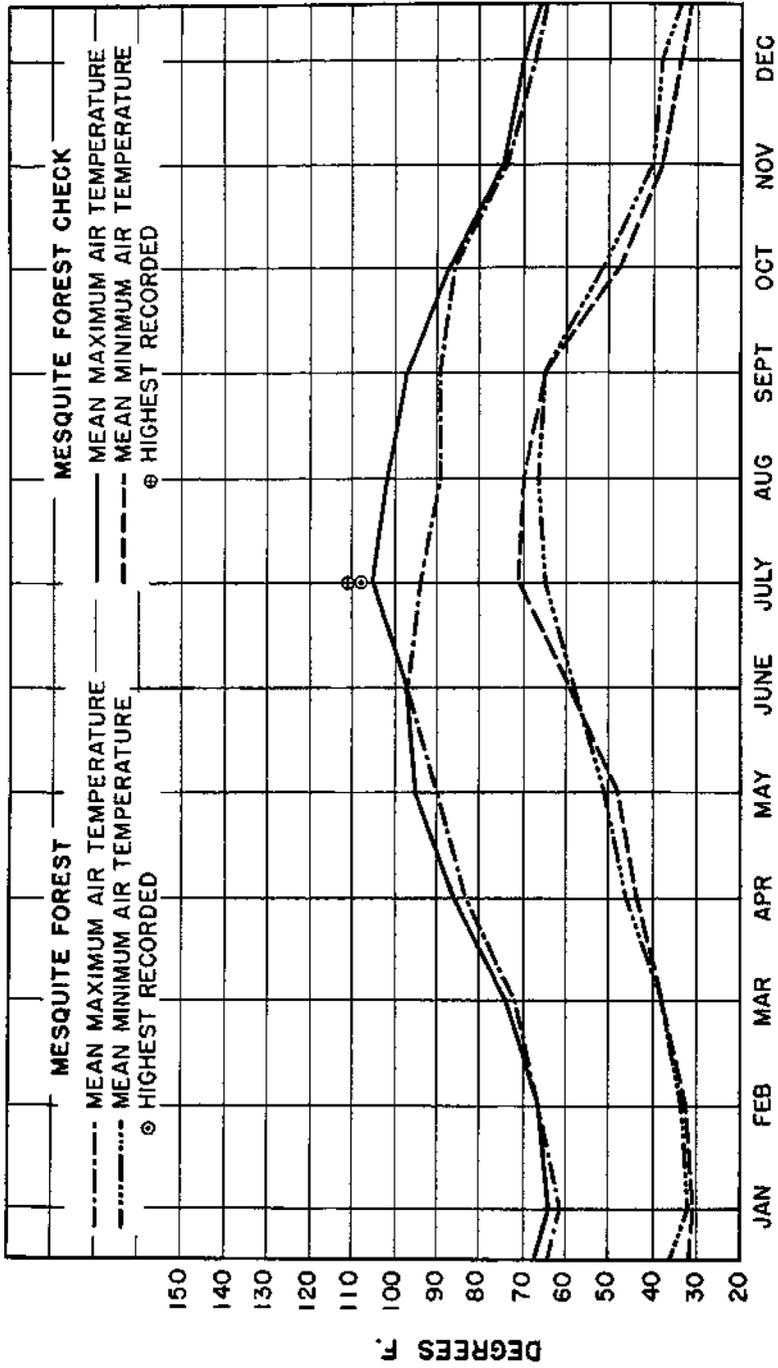


Figure 8—Air temperatures in mesquite forest, and "check" on adjacent desert

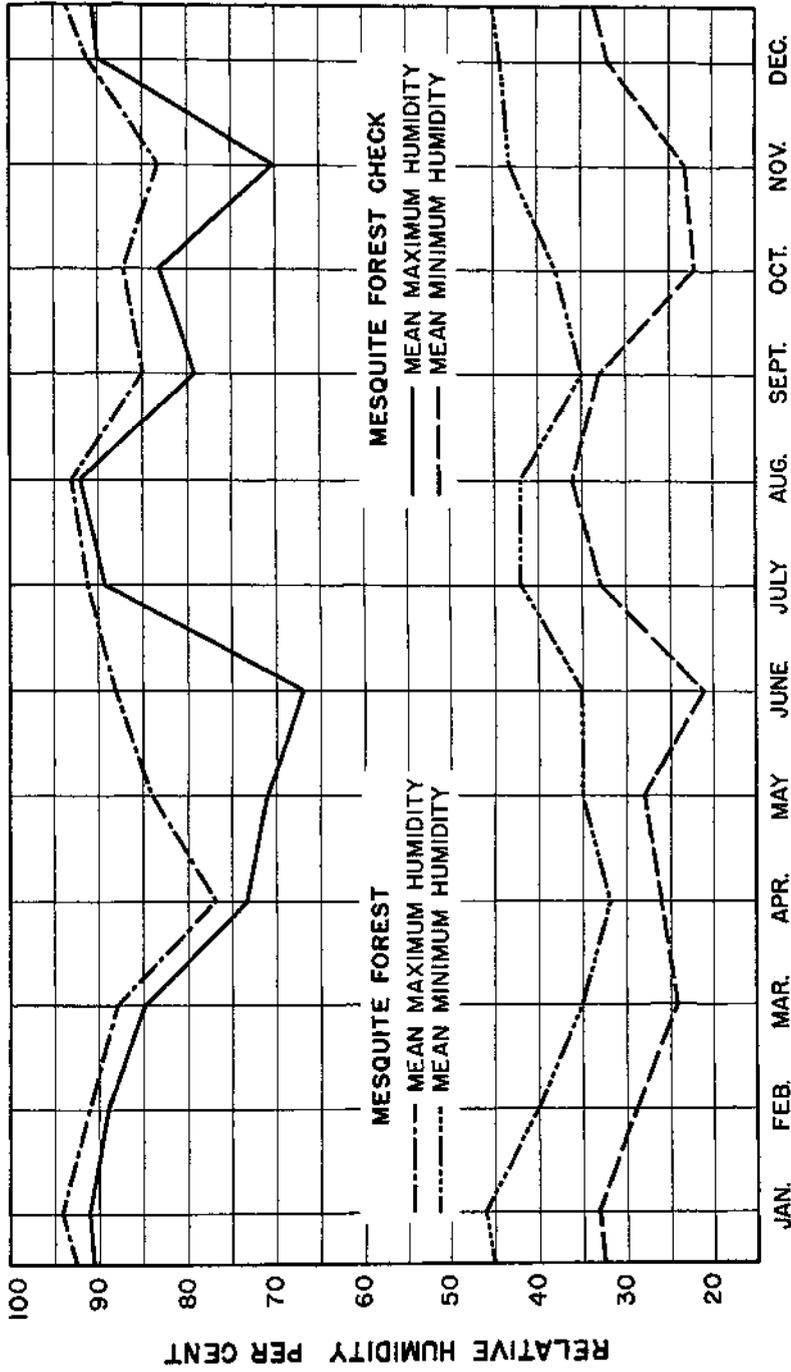


Figure 9.—Humidity in mesquite forest, and “check” on adjacent desert.

The mean minima curves show a fairly consistent parallelism as between forest and desert, the forest being at all times the moister situation. The closest parallelism is in the winter during the months that mesquite sheds its leaves and transpiration is least. A marked discrepancy in June results from the heat and lack of rain on the check, which is in marked contrast to the effects of the luxuriant fresh foliage of the forest. The divergence decreases in the period of summer rain and increases sharply in the dry, warm autumn months, the mesquite foliage remaining during this time.

The curves of mean maxima closely parallel each other during the leafless season for mesquite,<sup>7</sup> but diverge widely from the time the forest comes into leaf, the maximum humidity there rising steadily right through the arid foresummer, while it diminishes markedly in the desert. This may appear impossible, but the refreshing coolness of early morning in the mesquite forest, even in June, bears out the record. Summer rains increase the maximum humidity of the desert to a surprising extent.

These records indicate a climatic environment in the mesquite forest which certainly is conducive to conservation of body fluids for the animals which use the shelter of the forest. Certainly, by human standards of comfort, the mesquite forest is preferable to the wide open, shadeless desert.

However, the mesquite forests of southern Arizona are not used by most of our native rodent fauna as a means of conserving their precious water. Hardly any of them inhabit the mesquite forests exclusively, and very few divide their distribution between the protecting forest and the dry mesas.

Kangaroo rats and pocket mice are absent or few in numbers in the mesquite, those present being chiefly in the relatively open spots. *Neotoma albigula* is abundant in quite open cactus-rabbit brush-palo verde areas, almost absent from the grassy bajadas, and common but not abundant in the mesquite forest. *Citellus tereticaudus* is not found in the denser forest, but sometimes in quite open, scattered mesquite. Jack rabbits, it would seem, since they must remain above ground, should move into the shade of the mesquite forest, but in the denser, older forest they are seldom seen. To move for daytime shelter into such mesquite forests as that sampled in our study would require daily migrations of many miles from their present preferred feeding grounds.

On the other hand, on the great ranges of the Altar Valley, east of the Baboquivari Mountains, the antelope jack rabbits (*Lepus alleni*) do repair by day to the small strips of mesquite extending like fingers up the washes between the rolling, grassy hills. These hills are, or recently were, almost exclusively grass covered, giving a minimum of either concealment or shade for jack rabbits. The intervening strips of mesquite are not dense forests, nor are the trees large, and the strips are mostly narrow.

<sup>7</sup>December (in part), January, February, March, April (in part).

Probably the rodents and other nonforest animals, like humans, have other reasons than the relative comfort of the forest climate for not living there. Much as the human animal appears to enjoy the dim, cool depths of the forest, he does not, on the whole, like to remain permanently in it. When he moves into the forest, he first hacks out an opening to let in sun and "air." If he finds the exposure too severe, he replants with trees to the exact extent desired.

#### SUMMARY

1. The microclimates of selected desert mammals, living in the same general environment, were investigated by means of soil thermographs and hygrothermographs, supplemented by rain gauges, thermometers, and psychrometer.

2. The food habits of each species are correlated with its habitat and microclimate.

3. The kangaroo rat (*Dipodomys spectabilis*) eats mostly air-dry food, mainly seeds, with a minimum water content, yet the animal seldom if ever takes free water. Its deep burrowing and nocturnal habits and its physiology conserve water.

4. The wood rat (*Neotoma albigula*) does not drink, but uses more succulent food. It is less strictly nocturnal than *Dipodomys* and lives in a shallower and less well-protected burrow.

5. The round-tailed ground squirrel (*Citellus tereticaudus*) uses much succulent food and drinks when water is available. Its diurnal habit requires more moisture, which is partially compensated for by a deep burrow into which it may retreat during the hottest hours, and in which it lies dormant through the autumn drought.

6. The jack rabbits (*Lepus* spp.) are mainly nocturnal, but have no such shelter as a burrow against heat and desiccation by day. Only under most unusual circumstances do they drink, perhaps never in their normal existence. The more they need water, the less likely is it to be available. Their food is highly succulent, mainly mesquite and cactus, with the latter increasingly consumed as drought conditions increase.

7. A comparison of the climate of the mesquite forest with the adjacent desert mesa shows a less extreme climate in the forest, especially as to atmospheric humidity and soil-surface temperature. Nevertheless more mammals, both as to species and individuals, live in the desert environment. This is especially true of the Heteromyidae, the kangaroo rats and pocket mice.

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