FACTORS INFLUENCING THE DISTRIBUTIONS OF
TWO SPECIES OF *PEROGNATHUS*[1]

KENNETH D. HOOVER[2], WALTER G. WHITFORD, AND PAUL FLAVILL
Department of Biology, New Mexico State University, Las Cruces, New Mexico 88003 USA

Abstract. Perognathus penicillatus and *Perognathus intermedius* were studied in two areas in Doña Ana County, New Mexico, from 1970–1972. *Perognathus penicillatus* was associated with sandy soils and *P. intermedius* with soils composed of predominantly larger particles. Soils from areas where *P. intermedius* was found had a lower heat buffering capacity than soils from areas occupied by *P. penicillatus*. Artificial burrows when occupied by either species had a higher concentration of CO_2 in *P. intermedius* type soils. *Perognathus penicillatus* occupied burrows in cooler places, survived a narrower temperature range, and exhibited higher rates of evaporative H_2O loss with increased ambient temperature and CO_2 concentration than did *P. intermedius*. *Perognathus penicillatus* was the more aggressive species, and dominated *P. intermedius* in laboratory encounters.

Perognathus penicillatus can probably exclude *P. intermedius* from habitat that provides a burrow microclimate that the former can tolerate. *Perognathus intermedius* is physiologically able to survive in the more extreme habitat not suitable for *P. penicillatus*. The distribution of soil types and other microgeographical features that affect the burrow microenvironment, together with rainfall and temperature patterns, determine the areas where the two species will persist. The climatic variability of this desert site can result in changes in overall suitability of an area and hence in distribution and range of each species.

Key words: Behavior; burrow; competition; desert; New Mexico; Perognathus intermedius; *P. penicillatus;* respiration; rodent; thermoregulation.

INTRODUCTION

Perognathus penicillatus eremicus and *Perognathus intermedius intermedius* are morphologically similar heteromyid rodent species that overlap throughout much of their distribution in the southwestern United States and northeastern Mexico (Hall and Kelson 1959). Areas with one or both species occurring near the Desert Biome, Jornada Bajada Validation Site, presented an opportunity to look for the factors that account for their distributions.

The distributions of pocket mice (Bateman 1967; Wood 1969; Rosenzweig and Winakur 1969; Arnold 1942) and of other desert rodents (Reynolds and Haskel 1949; Reynolds 1950; Gaby 1972; Beatley 1969; Rosenzweig 1973) have been related to vegetation type. However, the distributions of many rodents have been related to soil types (Durrant 1943; Arnold 1942; Deynes 1954; Bateman 1967; Miller 1964). Hence, the occurrence of desert rodents in only certain vegetation types may be due to the dependence of vegetation on soil type. Clark and Otis (1952), Kennerly (1964), Hayward (1966), and McNab (1966) suggest that the particle size distribution of soils may determine the suitability of an area for a burrowing animal. Since variation in soil types affects the soil water holding capacity and its temperature characteristics (Penmon 1940*a*, *b*), burrow microclimate was investigated as a function of soil particle size distribution in an attempt to connect this environmental parameter with the

physiological adaptations of *P. penicillatus* and *P. intermedius* to a desert environment.

Many observations on small mammals (review by Grant 1972) suggest that behavioral interactions between species can be important in determining their distributions on a microgeographical scale. We investigated the outcomes of inter- and intraspecific encounters of the two pocket mice in the laboratory. Because of the difficulties in accounting for both the availability of and preferences for the food items of desert gramnivores, direct competition for food and possible niche separation by such parameters were not investigated. This study examines the importance of the physiological and behavioral traits of *P. penicillatus* and *P. intermedius* as causes of their observed habitat utilization under the varying conditions of a desert ecosystem.

MATERIALS AND METHODS
Live trapping

A site 40 km NNE of Las Cruces, Doña Ana County, New Mexico (T21S, R1E, S1) on the east slope of Mt. Summerford was chosen for a permanent trapping grid because it lay across separated populations of the two species. The grid was 80 m wide and 500 m long, consisting of four rows of traps with 20-m trap spacing. The grid traversed an area which had only *P. penicillatus* and an area which had only *P. intermedius*. Population data for sympatric populations of the two species was obtained from the trapping grid of the Desert Biome, Jornada Bajada Validation Site, ≈0.5 km SE of the first study area. The bajada grid was a 100-m square with 10-m trap spacing. Elevation for both sites is about 1,375 m.

Animals were trapped with folding Sherman live traps baited with rolled milo (grain sorghum). At Mt. Summerford trapping sessions were for 2 to 3 nights, once each calendar month for a period of 12 mo. Two traps were placed at odd-numbered stations on one night and at even-numbered stations on the next. Traps were set and baited about 90 min before sunset and checked at about sunrise the next morning, or at midnight during cold periods. Captured animals were uniquely toe-clipped and released at point of capture. Population estimates were made by the Lincoln Index. The standard errors of these estimates were calculated according to the formula given by Smith (1966). Trapping on the US/IBP grids followed a similar routine to that on the Mt. Summerford grid but was at bimonthly intervals from 1971–1973.

Vegetation

To determine the canopy cover of each plant species present, the Mt. Summerford grid was divided from N to S into twenty-five 20-m × 80-m sections. Each section was then subdivided into 4 equal parts, each further divided into twenty 1-m × 20-m segments. Two parts were selected at random from each section, and a segment then selected randomly from both of them. A 20-m line intercept was run in each selected segment. Data were grouped by grid section. Vegetation analysis for the Desert Biome grids was obtained from a 1971 Progress Report for the Jornada Validation Site (Whitford 1972).

Soils

To determine particle size distribution of soils, samples were taken at depths of 10 and 20 cm near burrows into which an identified animal had been followed at least twice. On Mt. Summerford samples were taken near 10 burrows of *P. intermedius* and seven burrows of *P. penicillatus*. Five samples from near the burrows of each species were taken from the US/IBP grid. Samples were sifted through soil screens with openings of 0.792, 0.566, 0.399, 0.282, 0.200, and 0.141 cm, dried for 20 h at 105°C, and weighed. During September 1972, soil temperatures were measured at 5 places on the Mt. Summerford grid. Thermistors were at a depth of 15 cm on both grids. Readings were taken at 1.5-h intervals with a soil test microammeter.

Behavior

Interspecific and intraspecific interactions of *P. penicillatus* and *P. intermedius* were observed in a chamber similar to that used by Eisenberg (1963). The plywood chamber was 183 cm × 66 cm × 61 cm high. Each partition housed a swinging door 30 cm × 30 cm which could be fastened up out of the way as desired. The bottom of each door was 31 cm from the bottom of the chamber and could be covered with a layer of soil. This provided an opening through which the animals could move. The chamber lid was hinged and consisted

of a large frame holding two large sections of glass. Two 100-W red light bulbs suspended 65 cm above either side of the lid illuminated the inside of the chamber. The chamber was filled with soil to a depth of 31 cm. Soil was obtained from the area where both species were captured. An animal was placed in each end section of the chamber with doors of the partitions closed. The red overhead lights were turned on and the room lights turned off. About 1 h was allowed for the animals to familiarize themselves with the test chamber. During this time their actions were observed. The swinging partition doors were fastened open and a layer of soil brushed over the base of each opening. Observations were made of the interactions of the animals. Observations were made between 1800 and 2300 h local time. The animals used had been in the laboratory at room temperatures (20–22°C) with a 12-h LD photoperiod for 5 to 6 mo. They were housed individually in high plastic mouse cages which contained a layer of soil and a paper towel. They were fed rolled milo *ad libitum*.

Burrow microclimate

To determine how burrow microclimate is affected by soil types and occupancy by each species, 2 identical artificial burrows were constructed. Burrow design was based on the morphology of 5 excavated burrows of each species. Burrows of the two species were similar. Artificial burrows were of hardware cloth covered with screen. They consisted of a tunnel (33.5 cm × 3.5 cm diameter) leading into a nest chamber (6 cm × 8 cm × 4.5 cm), which gave a total burrow volume of 538 cm³. The tunnel was curved so that the top of the nest chamber was parallel and 18 cm below the surface of the soil. Surgical rubber tubing (0.4 cm in diameter) and a thermistor were securely placed in the top corner of each nest chamber. The tubing and thermistor wires were accessible above the soil for taking burrow temperatures and air samples. One artificial burrow was placed in soil taken from near a natural burrow of each species. Soil and burrows were kept in chambers ≈60 cm on a side.

Percentages of O_2 and CO_2 in burrows were determined using a Unico™ No. 440-10 gas detector kit. This apparatus required air samples of 55 cm³ per O_2 determination and 100 cm³ per CO_2 determination. Kitagawa™ oxygen tubes (No. 159A, 2–30%) were used for O_2 measurements and Kitagawa™ high range carbon dioxide tubes (No. 120A, 0.1–2.6%) were used for CO_2 measurements. These tubes were accurate to ± 0.1%. Relative humidities were measured with an Atkins® gun psychrometer. A 1-min flushing period was necessary to draw a sample through the surgical tubing.

Three animals of each species, which had been in captivity for 3 to 4 mo, were used in each soil type. Measurements on the burrows of the first pair of animals were repeated several times during a period of 5 days to check for variation in the readings. Only

readings obtained during the 3rd through the 5th days were used in the analysis. For the second and third pairs of animals single measurements were taken in the morning and in the afternoon of the 3rd and 5th days that the animals occupied the burrows. Air samples of up to 100 cm³ would be withdrawm from the burrows without changing gas concentrations due to mixing with ambient air. Separate samples were taken to obtain relative humidities, O_2 and CO_2 concentrations, and the minimum quantity of air removed from the burrows during any one sampling period. When measurements had been obtained for *P. penicillatus* in *P. penicillatus* soil, and *P. intermedius* in *P. intermedius* soils, the animals were switched so that the same animals were in burrows of the opposite soil types. Animals had access to milo and lettuce during the experiments.

Physiology

The effect of temperature on O_2 consumption and evaporative H_2O loss was measured in a way similar to that described by MacMillen and Lee (1970). A flow-through chamber 75 cm³ in volume was made from 5-cm diameter glass tubing. Rubber stoppers pierced by glass tubing served as ends that allowed incurrent and excurrent passages for air. The chamber was placed in an incubator where the desired temperature had been determined to ± 1°C. A layer of mineral oil in the bottom of the chamber covered any feces or urine excreted by the animal which rested on a hardware cloth platform. Air dried over $CaCO_3$ and equilibrated with chamber temperature by passing through 2-m of Tygon® tubing in the incubator flowed through the chamber at 40 cm³/min. Air flow was monitored by a flowmeter and adjusted by a valve between the pump and flowmeter. Air leaving the chamber passed through Drierite® to absorb H_2O, and through tubes of Ascarite® to absorb CO_2. This air then passed through a flowmeter into a Beckman® flow-through paramagnetic O_2 analyzer.

The O_2 consumption and H_2O loss of five males and five females of each species were measured for 1 h at 5, 15, 25, 31, and 35°C. An animal was allowed to acclimate in the chamber at the experimental temperature for 1 h before the measurement period. At other times the animals were kept at 20–22°C. Water loss and CO_2 production were determined gravimetrically by weighing the Drierite® and Ascarite® after each 1-h run with a balance (± .01 mg). Oxygen readings were taken at 12- to 15-min intervals. These readings were averaged to calculate the volume of O_2 consumed by the animals. A CO_2 correction factor was obtained by running ambient air at 40 cm³/min through the system for 1 h. If an animal was torpid after a 1-h run, this was noted and those data were treated separately from data for normothermic animals.

To measure the effect of increased CO_2 concentration on the O_2 consumption and evaporative H_2O

loss of the two species, air with CO_2 contents of 0.31 and 0.71% were used in the described procedure. The two CO_2 concentrations used represent the range observed in artificial burrows used by the mice. Carbon dioxide concentration was controlled by introducing into the airflow, by way of a mixing flowmeter, the necessary amounts of a 2% CO_2, 98% air, gas mixture. Oxygen consumption and evaporative H_2O loss were measured for two males and three females of each species at each CO_2 concentration at a temperature of 25°C.

RESULTS
Live trapping

From September 1970 to August 1971, on the Mt. Summerford grid, the density estimates of each species based on the Lincoln Index ranged from 1 to 9 individuals per ha. There was no significant difference between estimated densities of the two species on any sample date. *Perognathus penicillatus* was only taken in the most easterly 13 sections. Sections (numbered E to W) 1 through 7 are on a sand-gravel slope dominated by *Larrea tridentata*. Cover by creosotebush averaged 26%, average total shurb and subshrub cover was 27%, and average total cover by forbs and grasses was 8%. Sections 8 through 13 were dominated by forbs and grasses with the exception of section 10 where a dense patch of *Guttierrezia* sp. provided 42.5% cover. Mean shrub and succulent cover was 6%. In these sections total mean forb and grass cover was 50%, of which an average cover of 31% was *Eriogonum abertianum neomexicana*, an annual plant which can reach heights of > 40 cm.

Perognathus intermedius was taken only on sections 14 through 23. Sections 14 through 18 were characterized by coarse gravel with forbs and grasses providing a mean cover of 25% (range 18–32). Except for section 14, *E. abertianum* did not provide more than 1% cover. On sections 14–18 shrub and succulent cover, which averaged 7%, consisted mainly of *Ephedra trifurca*, *Yucca elata*, *Prosopis glandulosa*, and *Guttierrezia* sp. Sections 19 through 21 were through a pocket of *Larrea tridentata* that provided a mean cover of 20%. Forbs and grasses in these sections averaged 14% cover. Sections 22 to 25 were over the rocky and boulder-strewn steep slopes of Mt. Summerford. On the US/IBP grids, estimated densities of *P. intermedius* increased from 0 individuals/ha in May 1971 to a maximum of 46 individuals/ha in October 1971, and were again at zero in July and November 1972. Estimated densities of *P. penicillatus* ranged from 4 to 12 individuals/ha in 1971 with the highest density in November 1972. Unlike the population estimates on the Mt. Summerford grid, the densities of the two species differed significantly in May, August, and October 1971. Considering only those stations where either species were captured in any year, observed numbers of joint-occurrences over the whole year in 1971 and 1972 were significantly less than expected. In terms
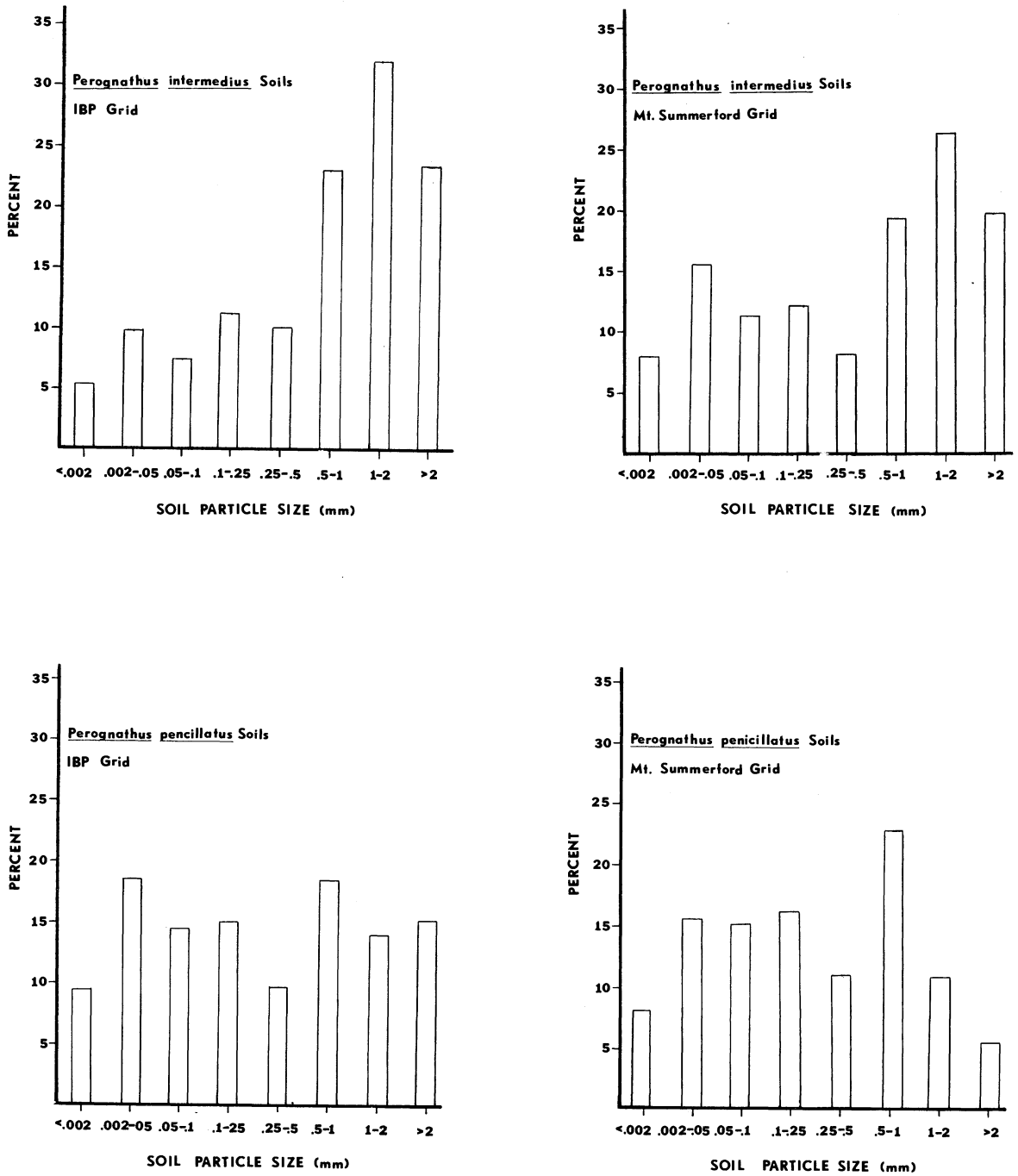
FIG. 1. Soil particle size distributions (percent by weight of the soil in each size group) from *Perognathus penicillatus* and *Perognathus intermedius* areas on the Mt. Summerford and US/IBP grids.

of number of stations utilized in 1971, *P. intermedius* was taken at 36, *P. penicillatus* at 31, and both species at 7. In 1972 *P. intermedius* was taken at 19 stations, *P. penicillatus* at 25, and both species at 4. Areas of heavy use by *P. intermedius* in 1971 were occupied by *P. penicillatus* in 1972. Only 3 of the joint-occurrences in each year were during the same trapping period. When looking at the occurrences of animals at stations

and their usage, it is difficult to relate it directly to vegetation cover: some stations where neither species were taken were to the human observer the same as stations where either one or both species were taken. The vegetation of the trapping grid is dominated by *Larrea* with 30% cover. Other shrubs, notably *P. glandulosa* and *F. cernua* along the major and minor arroyos, provided 2% and 1.71% total site cover, re-

spectively. Released *P. penicillatus* characteristically entered burrows close to the major or minor arroyos.

Soils

The combined top 20 cm of soil in areas occupied by *P. penicillatus* had consistently higher percentages by weight of smaller particle sizes than areas occupied by *P. intermedius* (Fig. 1). With the exception of the 0800 h record, when the average soil temperature of *P. penicillatus* soils was 20.5°C and that of *P. intermedius* was 20°C, mean soil temperatures on the Mt. Summerford grid in late September were always higher on *P. intermedius* type soils. The greatest difference of 2–4°C occurred between 1600 and 1800 h when both species would be confined to their burrows. At 1700 h mean soil temperature at 15 cm in *P. intermedius* soils was 30°C and was 26°C in *P. penicillatus* soils. On the IBP grids where temperatures were recorded year-round, the highest soil temperatures at 15 cm of 35°C occurred in July (Whitford 1971).

Behavior

Only actions repeated by most interacting pairs of animals are described. A detailed account is in Hoover (1973). Ten intraspecific interactions were observed for both *P. penicillatus* and *P. intermedius*. There were no differences in the kinds of intraspecific behavioral interactions shown by the two species. Encounters were characterized by aggression and pursuit by one animal and submission and retreat by the other. Fourteen different pairings of adult *P. penicillatus* and *P. intermedius* including all male-female combinations were observed. Interspecific encounters were characterized by (1) mutual aggression, (2) encounters occurring in the chamber initially occupied by *P. intermedius*, (3) *P. penicillatus* moving greater distances, (4) dominance and submission usually not being shown by the animals until after two or three encounters, when *P. penicillatus* would become the established aggressor, (5) *P. penicillatus* often leaving the section of the chamber originally occupied by *P. intermedius* after an encounter without being pursued and always returning for another encounter, and often being successful in chasing *P. intermedius* from its section of the chamber, and (6) *P. intermedius* always being driven from the *P. penicillatus* section of the chamber when it entered it. In all 14 pairings *P. penicillatus* showed more aggressiveness (pursuit of fleeing animals, and forcing more encounters) than did *P. intermedius*. No difference between encounters with the same or opposite sex were detected.

Burrow microclimate

In the field *P. penicillatus* often occupied burrows in soil which was shaded from direct sunlight during the warmest part of the day. Other burrows had openings in the vertical side of an arroyo with the shaft of the burrows proceeding down from that point. Some used
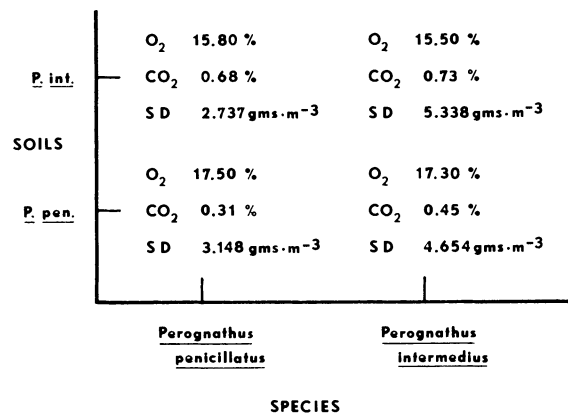

FIG. 2. Mean burrow microclimate readings of O_2, CO_2, and saturation deficit (SD) in all species-soil combinations in the artificial burrows.

burrows of larger heteromyid rodents which are deeper than those normally dug and occupied by *P. penicillatus* (Gaby 1972). Burrows shaded from direct sunlight or further from the surface of the soil would not experience the temperature extremes of burrow nest chambers nearer the surface of unshaded soils. Many animals used more than one burrow and one animal used three during the summer of 1972. Some *P. intermedius* entered burrow openings in the middle of *Opuntia* sp. stands. Other burrow openings used were under or near large boulders on the Mt. Summerford grid at the bases of *Larrea tridentata* shrubs, while some burrow openings were found in the opening away from boulders and vegetation.

During occupancy by either species, the average air temperature within the artificial burrows was 27.4°C (ambient 22°C). Figure 2 shows the differences in burrow microclimate parameters by species and soils. The following differences of means were highly significant ($P < .01$) by Student's t-test. The saturation deficit in burrows occupied by *P. penicillatus* ($\bar{x} = 2.943$ g/m³) was lower than in burrows occupied by *P. intermedius* ($\bar{x} = 4.996$ g/m³). Percent O_2 in the burrow atmosphere was higher in burrows in *P. penicillatus* soils ($\bar{x} = 17.4\%$) than in burrows in *P. intermedius* soil ($\bar{x} = 15.5\%$), while percent CO_2 was higher in burrows in *P. intermedius* soil ($\bar{x} = 0.69\%$, maximum value .78%) than in burrows in *P. penicillatus* soil ($\bar{x} = 0.39\%$, minimum value .28%).

Physiology

Confined *P. penicillatus* became torpid at 15°C and died at T_a (ambient temperature) greater than 37°C. All of the *P. penicillatus* subjected to -5°C for 2 h died. No *P. intermedius* died at -5°C but some were torpid. All *P. intermedius* subjected to 38°C survived that temperature, but many died at 40°C. Hayden and Lindberg (1969) reported that *P. penicillatus* became torpid at 10–15°C and died if left at 5°C.
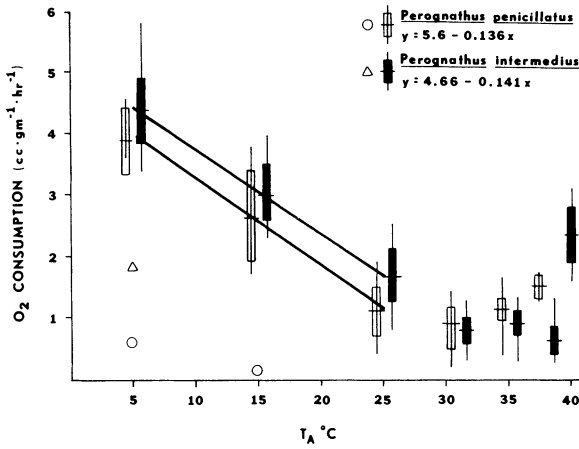
FIG. 3. O_2 consumption vs. ambient temperature (T_a) in two species of pocket mice. Vertical lines represent ranges, horizontal lines represent means, and rectangles enclose the 95% confidence limits for normothermic animals. The method of least squares was used to construct the two regression lines from the data for O_2 consumption below 30°C. Open circles and triangles represent mean values for O_2 consumption of torpid animals of *Perognathus penicillatus* and *Perognathus intermedius*, respectively.

FIG. 5. Mean evaporative H_2O loss for 5 animals of each species at 3 CO_2 concentrations. All measurements were taken at 25°C in dry air.

Rate of O_2 consumption by normothermic *P. penicillatus* and *P. intermedius* increased with decreasing T_a (Fig. 3). There was significant difference in O_2 consumption of *P. penicillatus* between 25°C and 35°C. There was similarly no difference for *P. intermedius* between temperatures of 31°C and 37°C. *Perognathus penicillatus* exhibited a wider and lower range of thermoneutrality than did *P. intermedius*. A linear regression line for O_2 consumption below 30°C for *P. intermedius* intercepted the abcissa at $T_a = 31.7$°C. Although the slopes of the two regression lines were
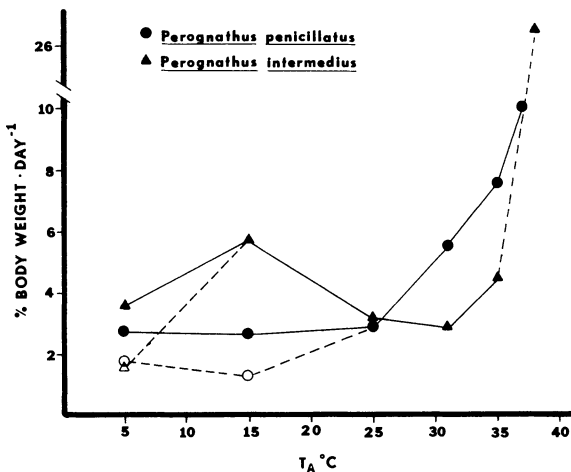

FIG. 4. Mean evaporative H_2O loss vs. ambient temperature (T_a) expressed as a function of body weight for torpid (open symbols) and normothermic (solid symbols) *Perognathus penicillatus* (circles) and *Perognathus intermedius* (triangles).
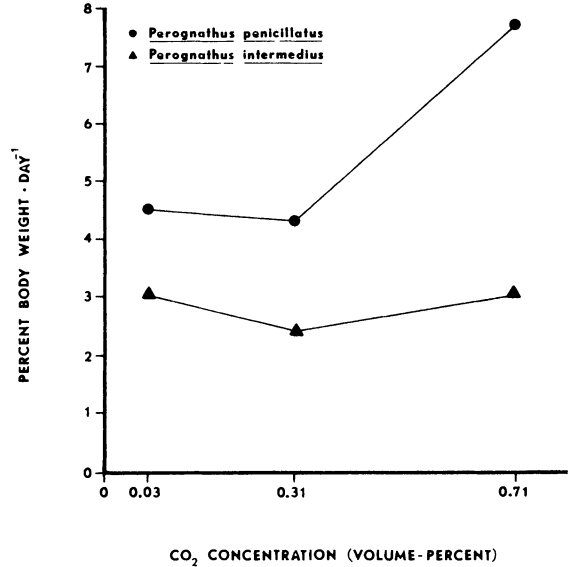
similar (Fig. 3), their elevations were significantly different ($P < .01$). Torpid animals were characterized by reduced O_2 consumption. Five of the *P. penicillatus* became torpid at 15°C. No *P. intermedius* were torpid at that temperature. At 5°C, 10 *P. penicillatus* and two *P. intermedius* were torpid.

Expressed as a function of body weight, the lowest loss of pulmocutaneous H_2O for *P. penicillatus* was at 5–25°C (Fig. 4), with no significant change in H_2O loss below 25°C. At temperatures above 25°C, H_2O loss in *P. penicillatus* increased rapidly to 10.1% of total body weight per day at 37°C. *Perognathus intermedius* showed the lowest H_2O loss at 5, 25, and 39°C. Water loss for this species was significantly higher at 15, 35, and 38°C than at 5, 25, and 31°C. At 38°C, H_2O loss was 26.62% of total body weight per day. It is not known why H_2O loss in *P. intermedius* increased markedly at $T_a = 15$°C. Torpid animals lost less H_2O than normothermic animals at the same temperature. Water loss as a function of body weight was significantly different between the two species at $T_a = 31$°C ($t - 2.15$, $P < .05$). Figure 5 shows pulmocutaneous H_2O loss at different CO_2 concentrations for the two species. There was a significant difference in pulmocutaneous H_2O loss between CO_2 concentrations of 0.31% and 0.71% ($t = 61.34$, $P < .01$) for *P. penicillatus*. The corresponding change in O_2 consumption from 0.98 to 1.1 cm³ per gram per hour was not significant. *Perognathus intermedius* did not significantly increase its H_2O loss with increase in CO_2 concentration, nor was the corresponding decrease in O_2 consumption of 0.1 cm³ per gram per hour significant. Evaporative H_2O loss at 0.31% was not significantly different from that at ambient (0.03%) CO_2 for either species.

DISCUSSION

The observations that need to be accounted for are the separation and similar densities of the two species on the Mt. Summerford grid, and changes in densities and area occupied by the two species on the US/IBP grids. The agreement of habitat usage by *P. penicillatus* with vegetation cover is not as clear as that found by Rosenzweig and Winaker (1969). The presence of *penicillatus* in areas lacking vegetation >45 cm high and its absence from the creosotebush area in sections 19 to 21 suggest that vegetation cover does not simply account for its distribution. The shifts in areas occupied by either species on the Bajada grid preclude any simple correlation with the dominant vegetation type.

Soil occupied by *P. penicillatus* consistently had a greater percent, by weight, of small particle sizes than soils occupied by *P. intermedius*. Higher CO_2 concentrations were recorded in burrows in the soil type associated with *P. intermedius* when occupied by either species. Such soil types in the field also showed greater extremes of temperature at depths where burrows are located than did the soil types associated with *P. penicillatus*. *Perognathus intermedius* tolerates both higher and lower temperatures, and can conserve water at higher T_a and CO_2 concentrations than *P. penicillatus*. *Perognathus intermedius* has the physiological attributes to tolerate the more extreme burrow microclimate. However, the ability of *P. penicillatus* to select the most favorable burrow location determines the overall suitability to that species of an area with a patchy distribution of soils. The burrow microclimate is a function of soil type and microgeographical features. Climatic variables affecting soil properties, such as temperature and soil moisture, will change the suitability of an area to each species. It is probable that such an effect ultimately caused changes in distribution of the two species on the IBP bajada grid between 1971, a dry year, and 1972, a wetter year.

The remaining ingredient to be included is the effect of interspecific interaction. Schroder and Rosenzweig (1975) have suggested that the distribution and population sizes of two *Dipodomys* sp. are determined more by habitat selection than by interspecific contest for habitat. It is possible in this case that habitat selection based perhaps on the quality of burrow environment would account for the two species distributions. However, the laboratory behavior of the two species show that interspecific aggression and contest are obvious elements of their behaviors and ultimately can explain why *P. intermedius* does not occupy habitats that its physiological traits would allow it to tolerate. If *P. penicillatus* can exclude *P. intermedius* from areas which the former can tolerate, then the distribution of the two species is a result of the interaction of soil structure and climate which determine burrow climate. Heterogeneity of soil types on the US/IBP grid allow the cooccurrence of the two species in a small

area, and climatic changes can change the areas occupied by each species. A more homogenous area in terms of soil type would be less likely to show change in the two species' distribution in response to climatic change. This would be the case on the Mt. Summerford grid.

This model which takes into account the physiological traits of the two species, the physical environment in which these traits would be important, the behavior of the two species, how their environment could be affected by climate, and the behavior of the two species may be of use in explaining the occurrence of these two species in other parts of their ranges.

LITERATURE CITED

Arnold, L. W. 1942. Notes on the life history of the sand pocket mouse. J. Mammal. 23:339–341.

Bateman, G. C. 1967. Home range studies of a desert nocturnal rodent fauna. Ph.D. thesis, University of Arizona. Univ. Microfilms, Ann Arbor, Michigan. 99 p.

Beatley, J. C. 1969. Dependence of desert rodents on winter annuals and precipitation. Ecology 50:721–724.

Clark, R. T., Jr., and A. B. Otis. 1952. Comparative studies on acclimatization of mice to CO_2 and to low O_2. Am. J. Physiol. 164:255–294.

Deynes, H. A. 1954. Habitat restriction and digging ability of certain pocket mice. J. Mammal. 35:453.

Durrant, S. D. 1943. General notes—*D. deserti* in Utah. J. Mammal. 24:404.

Eisenberg, J. F. 1963. The behavior of Heteromyid rodents. Univ. Calif. Publ. Zool. 69:1–114.

Gaby, R. 1972. Differential niche utilization by two species of kangaroo rat (Genus *Dipodomys*). Ph.D. thesis, New Mexico State University, Las Cruces. 71 p.

Grant, P. R. 1972. Interspecific competition among rodents. Annu. Rev. Ecol. Syst. 3:79–106.

Hall, E. R., and Kelson, K. R. 1959. The mammals of North American. 2 Vols. The Ronald Press Company, New York. 1,083 p.

Hayden, P., and R. G. Lindberg. 1969. Circadian rhythm in mammalian body temperature entrained by cyclic pressure changes. Science 164:1289–1290.

Hayward, J. S. 1966. Abnormal concentrations of respiratory gas in rabbit burrows. J. Mammal. 47:723–724.

Hoover, K. D. 1973. Some ecological factors influencing the distributions of two species of pocket mice (Genus *Perognathus*). Ph.D. diss. New Mexico State University, Las Cruces.

Kennerly, T. E., Jr. 1964. Microenvironmental conditions of the pocket gopher burrow. Tex. J. Sci. 16:395–441.

MacMillen, R. E., and A. K. Lee. 1970. Energy metabolism and pulmocutaneous water loss of Australian Hopping Mice. Comp. Biochem. Physiol. 35:355–369.

McNab, B. K. 1966. The metabolism of fossorial rodents: a study of convergence. Ecology 47:712–733.

Miller, R. S. 1964. Ecology and distribution of pocket gophers (Geomyidae) in Colorado. Ecology 45:256–272.

Penmon, H. L. 1940*a*. Gas and vapor movements in the soil. I: The diffusion of vapors through porous solids. J. Agric. Sci. 30:437–462.

————. 1940b. Gas and vapor movements in the soil. II: The diffusion of CO_2 through porous solids. J. Agric. Sci. 30:570–581.

Reynolds, H. G. 1950. Relation of Merriam kangaroo rats to range vegetation in southern Arizona. Ecology 31:456–463.

Reynolds, H. G., and H. S. Haskel. 1949. Life history notes on Price and Bailey pocket mice in southern Arizona. J. Mammal. 30:150–156.

Rosenzweig, M. L. 1973. Habitat selection experiments with a pair of coexisting Heteromyid rodent species. Ecology 54:111–117.

Rosenzweig, M. L., and J. Winakur. 1969. Population ecol-ogy of desert rodent communities: habitats and environ-mental complexity. Ecology 50:558–572.

Schroder, G. D., and M. L. Rosenzweig. 1975. Perturbation analysis of competition and overlap in habitat utilization between *Dipodomys ordii* and *Dipodomys merriami*. Oecologia 19:9–28.

Smith, R. L. 1966. Ecology and field biology. Harper and Row, New York. 652 p.

Whitford, W. G. 1972. 1971 Progress Report, Jornada Vali-dation Site, Desert Biome, US/IBP.

Wood, J. E. 1969. Rodent populations and their impact on desert rangelands. N. M. State Univ. Agric. Exp. Stn. Bull. 555:1–17.