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The Burrow Environment of the Banner-tailed Kangaroo Rat, *Dipodomys spectabilis*, in South-central New Mexico

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ABSTRACT: The thermal environment of both natural and artificial burrows of *Dipodomys spectabilis* was moderate as compared to surface ambient conditions but was related to them. Burrow air temperatures were similar to, but not identical with, soil temperatures. Burrow humidity was generally near saturation and was related to both burrow temperature and surface ambient humidity. CO₂ concentration in kangaroo rat burrows was variable but was always higher than ambient. Burrow CO₂ concentration resulted from a complex of factors that included soil moisture and temperature and proximity of an animal. Surface wind velocity probably plays an important role in burrow ventilation. Burrow structure and soil characteristics influence environmental conditions of burrows.

INTRODUCTION

The burrow environment of rodents differs significantly from the aboveground environment, but may be strongly influenced by it (Kennerly, 1964; Olszewski and Skoczen, 1965; Studier and Baca, 1968; Vogel *et al.*, 1973). In this study we have attempted to characterize the burrow environment of the banner-tailed kangaroo rat, *Dipodomys spectabilis*. Surface air temperature (T_A), soil surface temperature (T_S), surface water vapor pressure ($P_{H_2O(S)}$), wind speed, and extra-burrow soil temperature and soil moisture at several depths have been measured and related to burrow air temperature (T_{BUR}), burrow water vapor pressure ($P_{H_2O(B)}$) and burrow CO₂ concentration in both natural and artificial burrows.

METHODS

The field portion of the study was conducted from August 1972 to May 1973 on the New Mexico State University Experimental Ranch, ca. 30 km NNE of Las Cruces, Doña Ana Co., New Mexico. The laboratory portion was conducted on the New Mexico State University campus in Las Cruces from December 1972 to August 1973. Because the study was conducted sequentially, only the May 1973 sampling dates overlap.

Five natural burrows studied were a labyrinth of runways as described by Vorhies and Taylor (1922). Two artificial burrows of 7-mm-mesh wire screen terminated at 40-cm depth and two at 60 cm in a large, subdivided box of soil. The closed end (nest chamber) of each

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burrow was fitted with a glass sampling tube of 10-mm bore that extended vertically to the surface. Sampling tubes were sealed when not in use. Total volume of each 60-cm burrow was approximately 6676 cm³ and of each 40-cm burrow, 5655 cm³. The nest chamber portion of each burrow had a volume of approximately 1571 cm³. The entire assembly was covered with a removable coarse wire screen top and placed in an open area between two wooden buildings. One adult rat was introduced into each burrow. Rats remained in good health on a diet of mixed bird seed ad lib., and occasionally fresh greens. Sampling of environments within both natural and artificial burrows was done at monthly intervals during the 2 hr before sunset. Natural burrow environments were sampled with a graduated tubular probe, 1 m long, that contained a wet- and dry-bulb thermistor and a copper tube for gas sampling. The probe was pushed vertically into a burrow system from the surface. Measurements were made in runways of each of three burrow systems at two or three depths between 10 and 90 cm. Carbon dioxide concentrations were measured with a Kitigawa gas sampler (0.5% - 2.6% CO₂) that drew 100 cm³ of burrow air through an indicator tube at the rate of 20 cm³·min⁻¹. Sampling dead space was minimized by aspirating 100 cm³ of burrow air through the sampling tube before each CO₂ sample. Temperature of unaspirated burrow air was measured with the dry-bulb thermistor. Relative humidity was measured by aspirating burrow air over the wet-dry thermistors with a battery-powered vacuum cleaner attached to the probe at the surface.

Artificial burrows were sampled through the permanently installed glass tubes. Burrow air temperatures were measured with a thermistor that was inserted through the tube to the level of the nest chamber, and CO₂ concentration was measured as in the field. Relative humidity in the artificial burrows was measured with an Atkins gun psychrometer that consisted of a small fan that drew air through a tube and over a wet-dry thermistor assembly. The steel tube of the psychrometer was attached to the burrow sampling tube for humidity measurements. The same precautions for reducing dead space that were used in the field were used at the artificial burrows. Approximately 12% (200 cm³) of the nest chamber volume was withdrawn for CO₂ sampling and 73% or more of the remaining 1371 cm³ was withdrawn during humidity measurements. Therefore, there was probably some dilution of nest chamber air with tunnel air during sampling, but no dilution with surface air.

All surface temperatures were measured with a flat "banjo" probe that allowed adequate surface contact for reliable determinations of soil surface temperature. A soil probe thermistor was used to measure the 10-cm soil temperature in the artificial burrow chambers. Ambient relative humidity and T_A were measured with the thermistor used to measure T_{BUR}. Relative humidities were obtained from the wet-bulb depression (Marvin, 1941) and converted to water vapor pressure (Weast, 1965). All thermistors used were checked against 0 C. Wind speed was measured with a Dwyer handheld wind meter (2 to 60

mi·h⁻¹). Wind speeds were recorded as a range and the median was used after conversion to km·h⁻¹. Wind speed and air temperature were measured within 5 cm of the soil surface at both natural and artificial burrows.

Soil water potential (soil moisture) and soil temperature were obtained from gypsum electrical resistance soil blocks (Kohnke, 1968) and attendant thermistors. Soil temperature and moisture measurements were read on a microammeter and converted to C and bars of pressure, respectively. One soil block and thermistor were placed at the depth of the nest chamber in each of the artificial burrow chambers. All blocks were allowed to equilibrate with the soil for 30 days before any measurements were made. Because of equipment problems, soil water potential and temperature were not obtained at every sampling date, and the blocks were not in place during the first four sampling intervals at the artificial burrows (Table 1). Primarily because of hysteresis effects in drying and wetting soils, soil blocks should be calibrated to the soil in which they are used (Baver, 1965). Because the calibration procedure was lengthy and difficult, our blocks were not so calibrated. Because the resulting error could be quite high (20% to 50%), our measurements should be regarded as indicative of general patterns only.

TABLE 1.—Average soil temperatures, T (C), and water potentials, Ψ (bars), associated with burrows of *Dipodomys spectabilis*

Artificial burrows						
Depth		16 May 1973	20 June 1973	18 July 1973	28 Aug. 1973	
10 cm	T	25.3	31.9	26.4	32.1	
	Ψ	
40 cm	T	25.4	30.6	
	Ψ	-0.5	-0.6	
60 cm	T	28.3	25.4	31.0	
	Ψ	-19.7	-0.7	-0.6	
Natural burrows						
Depth		16 Aug. 1972	30 Aug. 1972	8 Oct. 1972	20 Nov. 1972	21 May 1973
10 cm	T	32.7	15.4	27.0	8.5	26.7
	Ψ	-42.6	-0.5	-23.5	-0.5	-0.6
50 cm	T	27.6	26.3	24.1	9.9	26.0
	Ψ	-49.6	-0.6	-19.1	-0.5	-0.6
90 cm	T	26.3	25.1	23.2	11.1	21.7
	Ψ	-48.6	-102.3	-14.2	-0.5	-0.6

Simple and multiple linear regressions and simple correlation coefficients were calculated using standard techniques (Steel and Torrie, 1960). Means are presented ± 2 standard errors where appropriate. Unless stated otherwise, the 5% level of probability was chosen for all tests of significance.

RESULTS

Minimum T_{BUR} were recorded in the field in December and in the artificial burrows in February, and maximum temperature was measured in both natural and artificial burrows in August (Fig. 1). Burrow temperatures decreased with increasing depth. Soil and burrow temperatures measured at the nest chambers of the artificial burrows were similar, but soil temperatures were a little lower than T_{BUR} during summer and a little higher during winter (Table 1, Fig. 1). Field burrow temperature data for < 30 -cm and > 30 -cm depth, and soil temperatures measured at 10-, 50- and 90-cm depth were less clearly related. Burrow air temperatures at < 30 -cm depth (Fig. 1) were similar to mean 10-cm soil temperatures (Table 1). There was little difference between shallow soil and burrow temperature, on the average, except on 30 August when the 10-cm soil temperature was unusually low as the result of a rain. On one occasion, the mean T_{BUR} at > 30 -cm depth was 0.4 C warmer than the 50-cm soil temperature (Table 1, Fig. 1). On the balance of the dates, deep burrow temperatures averaged 2.8 C cooler than 50-cm soil temperatures.

Burrow temperatures varied directly as a function of either T_{A} or T_{S} . The relationship was not essentially different between natural and artificial burrows so the data were pooled for regression analysis relating mean burrow temperature to either T_{A} or T_{S} . The resulting regression equations are:

$$T_{\text{BUR}} = -2.12 + 0.88 T_{\text{A}}$$

$$r^2 = 0.868, \text{ sy.x} = 3.19 \quad (1)$$

$$T_{\text{BUR}} = 0.05 + 0.77 T_{\text{S}}$$

$$r^2 = 0.902, \text{ sy.x} = 2.73 \quad (2)$$

Both regressions were highly significant (T_{BUR} vs. T_{A} , $P < 0.005$; T_{BUR} vs. T_{S} , $P < 0.005$). No statistical analyses were performed on the soil temperature data because of small sample sizes.

Burrow water vapor pressure varied from 6.1 - 33.9 mm Hg and was closely correlated with burrow temperature at any depth (Table 2). Water vapor pressure was also correlated between depths in both natural and artificial burrows (Table 2), and there was a correlation between $P_{\text{H}_2\text{O}(\text{S})}$ and $P_{\text{H}_2\text{O}(\text{B})}$ in the natural burrows (Table 2). The correlation between surface and burrow $P_{\text{H}_2\text{O}}$ in the artificial burrows was reduced by a pair of points that corresponded to a day

with strong winds (median wind speed, $6.4 \text{ km}\cdot\text{h}^{-1}$). Because a single point can strongly influence the correlation coefficient for small samples (Steel and Torrie, 1960), there seems to be ample reason to reject the outlying points in this case, which would improve the correlation.

There was a strong relationship between the variables, $P_{\text{H}_2\text{O(B)}}$,

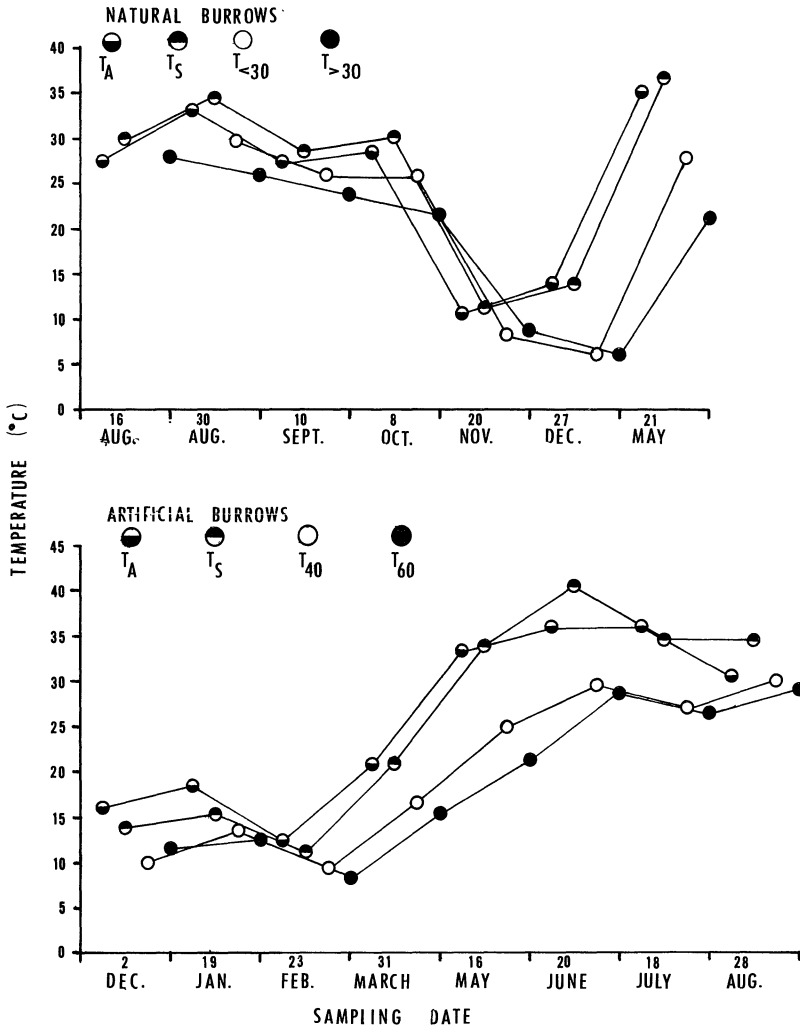


Fig. 1.—Air (T_A), soil surface (T_S) and burrow temperatures of natural and artificial burrows of *Dipodomys spectabilis*. Points represent means of from 2 - 4 temperature measurements. Temperature was measured at the depth, in centimeters, indicated by the subscript. Data points are placed at the end of the quarter of the month that contains the sampling date

T_{BUR} and $P_{H_2O(S)}$. The data from both artificial and natural burrows were pooled to obtain a multiple regression equation relating $P_{H_2O(B)}$ to T_{BUR} and $P_{H_2O(S)}$. The resulting regression equation,

$$P_{H_2O(B)} = -1.29 + 0.86 T_{BUR} + 0.09 P_{H_2O(S)} \quad (3)$$

$$R^2 = 0.939, \text{ sy}_{.12} = 2.18$$

is highly significant ($P < 0.005$).

Soil moisture was generally low but increased during winter (Table 1) as evaporation decreased.

In natural burrows, CO_2 concentration varied from 0.03 to 0.3% ($0.08 \pm 0.20\%$). Carbon dioxide concentration increased with depth in natural burrows (< 30-cm depth, $0.05 \pm 0.01\%$; > 30-cm depth, $0.09 \pm 0.03\%$) but tended toward a decrease with increased depth in the artificial burrows (40-cm depth, $0.97 \pm 0.41\%$; 60-cm depth, $0.43 \pm 0.19\%$). The lowest CO_2 concentration measured in the artificial burrows (0.07%) was obtained when the burrows were not occupied. Concentrations of CO_2 in the occupied artificial burrows were always greater than in the natural burrows. Carbon dioxide concentrations were correlated between depths in the natural burrows ($r = 0.901$, $P < 0.01$). Neither wind speed, $P_{H_2O(B)}$ nor T_{BUR} was correlated with CO_2 concentration in either natural or artificial burrows.

DISCUSSION

Maximum and minimum T_{BUR} measured during this study stayed

TABLE 2.—Correlation coefficients (r) between surface and burrow environmental variables from burrow of *Dipodomys spectabilis*

Artificial burrows							
Variable	T_A	T_S	$T_{BUR(2)}$	$T_{BUR(3)}$	$P_{H_2O(1)}$	$P_{H_2O(2)}$	$P_{H_2O(3)}$
T_S	0.979+						
$T_{BUR(2)}$	0.952+	0.981+					
$T_{BUR(3)}$	0.932+	0.964+	0.992+				
$P_{H_2O(1)}$	0.635	0.525	0.510	0.588			
$P_{H_2O(2)}$	0.854	0.911	0.954+	0.947+	0.484		
$P_{H_2O(3)}$	-0.453	-0.507	-0.543	-0.545	-0.008	-0.712	

Natural burrows							
Variable	T_A	T_S	$T_{BUR(2)}$	$T_{BUR(3)}$	$P_{H_2O(1)}$	$P_{H_2O(2)}$	$P_{H_2O(3)}$
T_S	0.979+						
$T_{BUR(2)}$	0.942+	0.958+					
$T_{BUR(3)}$	0.863+	0.886+	0.978+				
$P_{H_2O(1)}$	0.935+	0.919+	0.860+	0.779			
$P_{H_2O(2)}$	0.892	0.907	0.962+	0.976+	0.818		
$P_{H_2O(3)}$	0.752	0.775	0.901	0.967+	0.700	0.959+	

T_A = air temperature in C; T_S = surface temperature in C; T_{BUR} = burrow temperature in C; P_{H_2O} = water vapor pressure in mm Hg; + = significant correlation, $P < 0.05$

Natural burrows: 1 = surface; 2 = <30-cm depth; 3 = >30-cm depth

Artificial burrows: 1 = surface; 2 = 40-cm depth; 3 = 60-cm depth

well within the tolerance limits of *Dipodomys spectabilis* (Kay, 1975). It is likely that at the maximum depths of a kangaroo rat burrow complex the daily maximum temperature occurs at night (Baver, 1965; Kohnke, 1968) when the rat is foraging on the surface (Lockard and Owings, 1974). The vertical thermal gradient within a burrow system means that a kangaroo rat can select a location in the burrow at which thermal stress is minimized. Kenagy (1973) reported such intra-burrow temperature selection movements in *Dipodomys microps* and *D. merriami*. Only the extremely shallow burrows of some fossorial African rodents (McNab, 1966) have been reported to have thermal regimes approaching those of the surface. Other studies have shown that the thermal fluctuations within rodent burrows are modulated relative to the surface (Baudinette, 1972; Williams and Rausch, 1973; Soholt, 1974).

Soil physics (Baver, 1965; Kohnke, 1968) would suggest that all soil air spaces should be saturated with water vapor. Data presented by Schmidt-Nielsen and Schmidt-Nielsen (1950) indicated that a closed cavity in the soil was saturated with water vapor, even in dry soil. Relative humidities in burrows, however, may be as low as 50%-60% (Schmidt-Nielsen and Schmidt-Nielsen, 1950). On the days when the lowest burrow relative humidities were measured, in the present study, surface winds were strong with gusts up to about $16 \text{ km}\cdot\text{h}^{-1}$. Vogel *et al.* (1973) demonstrated that surface wind can induce measurable ventilation in rodent burrows depending on surface mound architecture. Southern New Mexico is notably windy especially in the spring months, and the structure of the burrow mounds of *Dipodomys spectabilis* (Vorhies and Taylor, 1922) is such that wind-induced ventilation probably does occur. Our data showing a regression relationship between $P_{\text{H}_2\text{O}(\text{B})}$ and $P_{\text{H}_2\text{O}(\text{S})}$ might be explained by wind-induced burrow ventilation. It is apparent that the low soil moisture measured during this study did not prevent the burrow air from being close to saturation most of the time, but there was no correlation between soil water potential and $P_{\text{H}_2\text{O}(\text{B})}$. Soil moisture was highest throughout the soil column during periods of lowest T_{BUR} and consequent low $P_{\text{H}_2\text{O}(\text{B})}$. During periods of high T_{BUR} and $P_{\text{H}_2\text{O}(\text{B})}$, soil moisture was variable, both through time and soil column (Table 1). The turnover rate of burrow air could be sufficient to reduce maximum $P_{\text{H}_2\text{O}(\text{B})}$ and establish gradients between $P_{\text{H}_2\text{O}(\text{S})}$ and $P_{\text{H}_2\text{O}(\text{B})}$ along the burrows. This latter observation could also explain the lack of correlation between soil moisture and burrow humidity.

The relationship among values of $P_{\text{H}_2\text{O}(\text{B})}$ at different depths and $P_{\text{H}_2\text{O}(\text{S})}$ indicates that there may be a moisture gradient within the burrow that, because of the dependence of saturation $P_{\text{H}_2\text{O}}$ on temperature, parallels the thermal gradient. We would, therefore, expect the daily and seasonal thermal shifts to be paralleled by moisture shifts in the burrow of *Dipodomys spectabilis*. The potential for behavioral responses to a vapor pressure gradient is apparent.

The drying power of burrow air, relative to a rodent, will depend

on the vapor pressure deficit between exhaled and ambient air. During periods of low temperature the burrow of a kangaroo rat would be potentially most stressful if exhaled air were near body temperature. The fact that *Dipodomys spectabilis* can reduce water loss by exhaling air at temperatures near ambient (Jackson and Schmidt-Nielsen, 1964; Collins *et al.*, 1971) suggests that the effect of reduced T_{BUR} (ca. 6 C) and $P_{\text{H}_2\text{O(B)}}$ (ca. 7 mm Hg) in winter will be minimized.

The relationship of CO_2 concentration in burrows to other physical parameters is apparently complex. From physical considerations of the soil, we would expect CO_2 concentration to increase with increased depth, decreased temperature and increased soil moisture due to changes in diffusivity (Baver, 1965; Kohnke, 1968). Our results do not agree with the expected results. Several explanations seem possible: (1) burrows may be so well ventilated, as discussed above, that CO_2 concentrations are constantly being mixed between burrow depths and the surface air; (2) burrows may not behave in the same way as smaller soil air spaces; (3) a respiring animal located near a sample point may elevate the measured values due to expired CO_2 buildup immediately around the animal; or (4) some combination of these factors may influence the CO_2 concentration measured. Our artificial burrows and those used by Studier and Baca (1968) were short, simple and of moderate depth, and samples were drawn from nesting chambers. We measured the environment as maximally modified by the resident animal. In both situations CO_2 concentrations were higher and temperatures more variable than in natural burrows where samples were drawn from runways and proximity to an animal was unknown. In the artificial burrows, the *Dipodomys spectabilis* were always within a few centimeters of the sampling point and CO_2 concentrations were several times higher than in natural burrows. However, when no rats were present in the artificial burrows, the mean burrow CO_2 concentration (0.07%) was nearly identical to that of the natural burrows (0.08%).

Shape, size, complexity and depth influence the burrow environment, as does soil type. Hooper and El Hilali (1972) described temperature differences between burrows of two species of jerboas (*Jaculus*) that seemed to be associated with differences in burrow shape, depth and soil type. Gaby (1972) described thermal and moisture differences between burrows of *Dipodomys ordii* and *D. merriami* that were related to soil type and burrow structure. Hoover (1973) described differences in CO_2 concentration between burrows of two species of pocket mice (*Perognathus*) that were associated with soil types. The complex natural burrows of *D. spectabilis* had lower maximal CO_2 concentrations than other natural burrows studied (Kennerly, 1964; Studier and Procter, 1971; Darden, 1972; Baudinette, 1974). It is, however, interesting to note that although the range varied considerably, the mean CO_2 concentration in all of the natural burrows was remarkably similar.

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