REPORTS

PERIODICITY AND ENERGETICS OF TORPOR IN THE KANGAROO MOUSE, MICRODIPODOPS PALLIDUS

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Abstract. The effects of three environmental temperatures and four food rations on the duration and periodicity of torpor were examined, the oxygen consumption of torpid and normothermic kangaroo mice was measured, and temperature profiles in their habitat were obtained during all seasons. Because of their fossorial and nocturnal habits, kangaroo mice need not face environmental temperature above 30°C or much below 0°C although temperatures in their Great Basin habitat normally fluctuate far outside this range. Torpidity affords a reduction in energy expenditure which increases as temperature decreases. At 5°C the oxygen consumption of torpid mice was less than one-sixtieth that of normothermic mice.

When the animals were given seeds in excess each day, none became torpid at either 17° or 6°C, but when the daily ration was reduced to 1.5 g all individuals became torpid. The per cent time torpid and the duration of torpor cycles varied inversely with temperature. At 6°C the time in torpor increased when the daily food ration was reduced from 1.5 to 0.5 g but decreased slightly when food in excess was made available at longer intervals. Periods of torpor varied from a few hours to several days. The time in torpor was related to environmental temperature and food supply in such a way that the mice maintained body weight and accumulated food stores under all conditions tested. This suggests that in nature Microdipodops can regulate periods of torpor so as to conserve its stored seeds during both chronic and acute shortages of food.

In many desert habitats, where leaf and seed production is low and restricted to a brief part of the year (and sometimes may not occur for several consecutive years), small herbivorous homeotherms must be able to carry out all essential functions on a fixed and limited energy supply. Strict homeothermy and sustained high levels of activity can be self defeating for small desert mammals. The small size of these animals imposes a high energy cost for thermoregulation and restricts their foraging to a limited area. Many desert rodents circumvent this problem by temporary abandonment of activity and homeothermy—by hibernating, estivating, or entering short recurrent periods of torpor that are independent of season.

Although the occurrence of these three patterns is well known qualitatively (see Hudson 1967 for a review), little quantitative information exists on the way metabolic expenditures are budgeted against a limited energy supply. It is known that food reduction will cause many rodents to undergo daily periods of torpor, and Tucker (1962, 1966) has shown that at a given temperature the duration of the daily period of torpor of Perognathus californicus is inversely related to the daily food ration.

Our purpose in the present study was to examine the energetics of a small mammal which must adjust to limited and fixed energy stores while dealing with a wide range of ambient temperatures. We selected Microdipodops pallidus because of its small size (10–14 g), its capacity to become torpid (Bartholomew and MacMillen 1961), and its ability to subsist exclusively on dry seeds. Kangaroo mice are restricted to aeolian sand dunes in the Great Basin of western North America where precipitation is scarce, temperatures fluctuate widely both daily and seasonally, and the food supply is erratic.

Methods

Environmental temperature.—Soil and air temperatures were measured with thermistors. Soil temperature profiles were made during all seasons to depths of 40 cm in the sand dunes occupied by kangaroo mice. Air temperatures were measured in the shade 20 cm above the ground.

Capture and maintenance.—Thirty-one kangaroo mice were captured during the fall, winter, and spring of 1967–68 in sand dunes approximately 13 miles north of Dyer, Esmeralda County, Nevada at an elevation of 4,900 ft. In the laboratory the animals were maintained in a controlled temperature cabinet on a daily photoperiod of 11 hr. Food consisted of a mixture of millet, rape, and oat seeds supplemented on alternate days with lettuce.

Oxygen consumption and body temperature.—The oxygen consumption of normothermic and torpid animals at 25°C was measured in an open circuit system using a Beckman G2 paramagnetic oxygen analyzer. Flow rates were 200 cc/min. Water and CO₂ were absorbed from the air stream. The animals being measured were housed in 200-cc glass chambers equipped with wire-screen platforms above a layer of mineral oil. Humidity and temperature inside the chambers were monitored using thermocouples and an electric humidity sensor. The ambient temperature was controlled to 0.1°C with an Aminco bacteriological incubator. Postabsorptive animals were exposed to each ambient temperature for at least 3 hr. The values used represent the minimum stable levels of oxygen consumption observed during the experimental period.

The oxygen consumption of torpid animals at 5° and 15°C was measured with a recirculating, closed-circuit,
A peristaltic pump circulated air at 100 cc/min, through the 200-cc glass respirometer chamber and through tubes containing Ascarite and Drierite for the absorption of CO₂ and water. Temperature was controlled and monitored as described above. The sealed system was calibrated at constant temperature with the animal in the chamber by withdrawing a known volume of air with a hypodermic syringe, the needle of which was inserted into the respirometer through a serum stopper. During calibration and when the manometer was being read, the recirculating pump was turned off briefly. Between periods of measurement and until the animals became torpid, valves were opened so that dried room air was pumped through the system. After the animals became fully torpid, oxygen consumption was measured for 1–3 hr depending on the temperature. All values of oxygen consumption of torpid and normothermic mice were reduced to STP.

Body temperature was measured with vinyl-sheathed 30-gauge copper-constantan thermocouples connected to a potentiometric recorder. The thermocouples were inserted into the esophagus to a depth of at least 2 cm at the conclusion of each period of measurement of oxygen consumption.

**Torpor cycles.**—All measurements were made in a 12-ft³ refrigerator which controlled temperature to within 1°C. The lights were on for 11 hr each day. The animals were housed individually in fiberglass boxes (20 by 25 by 15 cm) containing 2 cm of dune sand and an artificial burrow (an opaque plastic tube of length 10 cm; I.D., 4.8 cm; O.D., 5.8 cm). One end of the burrow was sealed and the other was half occluded. To monitor the periods of torpor we used a simplified version of the technique developed by Tucker (1962). A thermocouple was mounted at the center of the sealed end of the plastic tube in such a way that the junction extended 2 mm into the cavity of the burrow. The thermocouples were attached to a multichannel potentiometric recorder to give a continuous record from five or six cages containing mice and one empty cage. From the temperature records we could determine the onset and termination of torpor of each mouse. When the burrow was occupied by a normothermic animal the burrow temperature was 2–5°C higher than when the animal was torpid or outside the burrow. Periods when the animals were torpid and in the burrows could be distinguished from those during which the animal was active but outside the burrow by rates of temperature change. Active animals left and entered the burrow frequently and caused abrupt changes in the temperature. When an animal became torpid the decline in burrow temperature took an hour or more.

When a mouse aroused from torpor the rise in burrow temperature was also gradual.

Our experimental design was simple. We exposed the mice to three ambient temperatures (17°C, 11°C, and 6°C) and gave them four rations of unhulled seeds (food presented daily in excess, 1.5 g/day, 0.5 g/day, and 21 g at intervals of 1 week). After the last two experiments the sand was sifted and the seeds obtained were weighed.

**RESULTS**

**Field observations.**—Kangaroo mice are active at night on the surface at all seasons of the year, even when temperatures are 10°C or more below freezing. However, under special circumstances they may remain below ground for several consecutive nights. For example, in January 1968, in our study area, heavy precipitation followed by a series of cold nights produced a continuous mantle of frozen sand at least 40 cm thick over the entire dune area. In 2 consecutive nights of trapping during the freeze no kangaroo mice were captured in 50 traps. In the same area in winter when the sand was not frozen but temperatures were within a degree or two of freezing, trapping success for *Microdipodops* was approximately 20% of traps per night.

In the habitat of *Microdipodops* air temperatures fluctuated widely both daily and seasonally while soil temperatures at depths of 20 and 40 cm showed almost no daily fluctuation but varied over a range of 25°C to 28°C seasonally (Fig. 1). Because of their fossorial and nocturnal habits, kangaroo mice probably need not encounter ambient temperatures above 30°C even in midsummer. In winter, by remaining in their burrows on the coldest nights and otherwise confining their activities to the period immediately after sunset, kangaroo mice can evade the extremes of cold characteristic of their macroclimate but they cannot avoid temperatures slightly below freezing.

**Energetics of torpor.**—The oxygen consumption of normothermic kangaroo mice was linearly and inversely related to ambient temperature between 5°C and 25°C, whereas that of torpid animals was exponentially and directly related to ambient temperatures within this range (Fig. 2). The esophageal temperatures of normothermic mice at the end of the oxygen consumption measurements ranged from 31.7°C to 37.0°C at ambient temperatures from 5°C to 25°C. At an ambient temperature of 35°C the animals were slightly hyperthermic with body temperatures of 37.5°C to 39.0°C. Torpid mice had esophageal temperatures from 1.0°C to 3.5°C above ambient with the greatest differences being found at the lowest ambient temperatures.

![Fig. 1. Daily and seasonal changes in the temperature of the air and of the soil 20 and 40 cm below the surface in the sand dune habitat of *Microdipodops*.](image-url)
Fig. 2. The relation between oxygen consumption and ambient temperature in normothermic (circles) and torpid (crosses) kangaroo mice. A least-squares regression line has been fitted to the data for normothermic mice at ambient temperatures below 30°C and its slope (b) is given. There was little variation in the metabolism of torpid mice at a given temperature so only the means have been plotted; sample sizes are given in the parentheses.

It is clear from Figure 2 that torpidity allowed a marked reduction in energy expenditure, and this savings increased as ambient temperature decreased. At 5°C the oxygen consumption of torpid mice was less than one-sixtieth that of normothermic mice. At 25°C the comparable fraction was approximately one-fourth.

Influence of food and temperature on body weight and torpor cycles.—The effects of sequential experimental manipulations of ambient temperature and food on the body weights of five individuals are shown in Figure 3. The patterns of torpor in these same individuals were recorded automatically, and the data obtained are presented in Figures 4 and 5. Six additional mice were subjected to the same experimental regime and weighed periodically. Their body weights showed the same pattern of variation as those of the animals depicted in Figure 3. Owing to the availability of only a single six-channel recorder, the pattern of torpor in the six additional animals could not be measured quantitatively, but daily observations indicated that their patterns did not differ significantly from those of the mice reported below.

On all treatments, body weight remained essentially equal to or exceeded the weight at capture (Fig. 3). It is of interest that the pelage of the animals remained in much better condition at 6°C and 11°C than at 17°C.

When food was available in excess, none of the kangaroo mice became torpid at either 17°C or 6°C (Fig. 5). When the food ration was reduced to 1.5 g of seed given daily, every individual became torpid at each of the three test temperatures (Fig. 4). Both the per cent of time in torpor and the duration of the torpor cycles increased as temperature decreased. Periods of torpor usually lasted between 7 hr and 3.5 days. The intervals between periods of torpor were variable but were rarely less than 5 hr. Arousals typically occurred shortly before the
beginning of the daily dark period. The record of a typical individual is shown in Figure 6.

When temperature was held constant at 6°C and the food ration was varied, the mice responded by altering their patterns of torpor. When the amount of food given daily was reduced from 1.5 to 0.5 g, the per cent of time in torpor and the mean duration of each period of torpor increased (Fig. 5).

The torpor cycles of animals at 6°C were followed for 3 weeks and 21 g of seed (bulk food ration) were placed in each cage on days 1 and 8. Despite the fact that food was initially available in excess, all animals continued their cycles of torpor; the periods of torpor were slightly shorter than when 1.5 g of food were supplied daily. However, when food in excess was given each day, rather than at intervals, none of the mice became torpid.

At all temperatures and on all food rations the mice cached stores of seeds in their cages. On a given regime of food and temperature the amount of food stored was directly related to the amount of time spent in torpor (Fig. 7). Even the animals given only 0.5 g per day stored from one-fifth to two-thirds the food they received during the 16 days of that experiment.

DISCUSSION

Microdipodops pallidus has a pattern of recurrent torpor which is intermediate between the prolonged periods of dormancy shown by hibernators such as marmots and ground squirrels and the daily torpor of temperate zone bats and a few small rodents such as Perognathus californicus. The length and periodicity of torpor in Microdipodops is related to both environmental temperature and food supply in such a way that the mice are able to maintain body weight and accumulate food stores under a variety of conditions. Like P. californicus (Tucker 1966), kangaroo mice show a feedback mechanism coupling energy demands and energy resources. But unlike P. californicus, which has only been shown to adjust the duration of its daily torpor to food availability at a given environmental temperature, Microdipodops integrates the energy supply of a variable food regime with the energy cost of activity and temperature regulation over a range of environmental temperatures. Its torpor is particularly advantageous because as ambient temperature decreases the energy required to maintain homeothermy increases, but the energetic cost of torpor decreases, so that Microdipodops can remain torpid longer on a given food ration. It remains torpid for several days under conditions of restricted food availability and low ambient temperature. Thus, Microdipodops achieves even more independence of environmental conditions than has been demonstrated in other small rodents. Under natural conditions it should be able to adjust its energy expenditures to conserve its food stores during both chronic food shortages resulting from failure or exhaustion of a seed crop and acute shortages owing to brief periods of inclement weather.

The range of temperatures over which kangaroo mice can enter and arouse from torpor (5°–25°C) falls within the annual range of deep-soil temperatures which we recorded in their habitat. The minimum environmental temperature at which torpid Microdipodops can arouse is less than 5°C—an unusually low figure for rodents weighing less than 20 g. This matching of capacity to arouse from torpor with lowest ambient temperature to which they are normally exposed has obvious selective
value and has been reported in a number of species of rodents (see MacMillen 1965 for summary).

Under the experimental procedures employed, a persistent circadian rhythm of arousal of the sort found by Chew, Lindberg and Hayden (1965) in several species of Perognathus would not be apparent. However, the mice tended to arouse shortly before the onset of darkness regardless of how long they had been torpid. Similarly Perognathus californicus (Tucker 1966) and Dipodomys merriami (Carpenter 1966) tend to arouse from their daily bouts of torpor before the beginning of the dark period. Under natural conditions such a timing of arousal would afford maximal conservation of energy and a maximal nocturnal period for foraging.

An unexpected outcome of the present study was the demonstration that kangaroo mice are able to integrate a complex of factors relating to environmental conditions and food supply and to match their energy expenditures to the total situation. On all food and temperature regimes the mice managed to maintain weight and store food. The bulk food experiments suggest that the duration and periodicity of torpor is keyed not only to the amount of stored food but also to the rate at which new food becomes available. Under natural conditions such a response should adjust the pattern of torpor to foraging success. In this respect kangaroo mice show behavior similar to, but more complicated than that reported for the hamster, which readily enters hibernation only after it was accumulated substantial food stores (Lyman 1954). Although flying squirrels rely primarily on construction of nests, curtailment of activity, and huddling of several individuals rather than torpor (Muul 1968), they are remarkably similar to Microdipodops in their ability to accumulate food stores and then adjust behavior and physiology to conserve these stores during times of food shortage and low environmental temperatures.

**LITERATURE CITED**


