

Bioenergetics of the Great Basin Pocket Mouse, *Perognathus parvus*

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Ingestion rates and annual energy expenditure for the Great Basin pocket mouse, *Perognathus parvus*, were studied in south-central Washington (Hanford Reservation) during 1970—71 as part of the US/IBP Desert Biome program. Food intake models were derived in relation to time, microenvironmental temperatures, metabolic rate, and coefficient of digestibility. Estimated annual ingestion rates were 2550 and 2462 kcal/yr for individual males and females, respectively. Summer torpor reduces these costs about 3%. Winter energy expenditure was 40—43% lower than summer because of more extensive periods of torpor. Estimated daily maintenance energy requirements ranged from a low of 2.36 and 2.63 kcal in the winter to a high of 6.96 and 6.55 kcal in the spring for individual adult males and females, respectively. These estimates indicate *P. parvus* consumes between 4—10% of its body weight in food per day during the year. Assuming a diet consisting entirely of cheatgrass seeds (*Bromus tectorum*), individuals require 873—999 seeds per day in the spring and summer, decreasing to about 775 seeds per day in the fall. In the winter, facultative torpor reduces this to less than 400 seeds per day, necessitating the caching of approximately 50—65 g of seeds. The average annual seed crop would support a maximum density of about 80 animals/ha, indicating this granivore may be periodically food stressed. The overall impact of *P. parvus* on plant succession at the Hanford site is probably minor.

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1. INTRODUCTION

Energy flow or total assimilation of energy by a population is a fundamental and unifying concept in animal ecology. With the advent of the International Biological Program (IBP), research efforts to estimate

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and model energy flow in the various biomes greatly increased (for review, see Petruszewicz (ed.) 1967, Petruszewicz & Ryszkowski (ed.) 1969 and Petruszewicz & Macfadyen (ed.) 1970).

Deserts occupy about one-third of the earth's land surface and represent a unique area to investigate energy flow in small mammal consumers. Desert communities have relatively few component populations and their simplified organization offers an opportunity for comprehension of the bioenergetics of a complete system (Chew & Chew, 1965). The Great Basin, with its sagebrush and grass vegetation, comprises the largest desert in the United States. As rodents are a notable element in the consumer population of this arid region, the study of their bioenergetics is important to the understanding of the variability and magnitude of energy transfer by small mammals in a »cold desert« ecosystem.

This paper examines the bioenergetic aspects of the Great Basin pocket mouse, *Perognathus parvus*, a granivorous heteromyid that is a common rodent in the northern Great Basin desert ecosystem. Based on laboratory and field studies, first-order estimates of this species' annual energy expenditure are made using a food-intake model. The effects of its energetics on the ecosystem are discussed.

To succeed under the harsh restrictions of the desert environment, heterotherms must maintain a balance between the food resources available in the habitat and the caloric and mineral demands necessary to sustain the appropriate activity for survival and successful reproduction. Aspects of this problem involve both behavioral and physiological adaptations.

Energy flow at any level within an ecosystem (e.g., species, population, community) complies with the general equation:

$$E_f = E_m + E_p \quad (1)$$

where E_f is total energy flow, E_m is total »cost« of maintenance and E_p is total »cost« of production (growth and energy storage) for a given time period. In turn, total maintenance (E_m) is the sum of energy dissipated at rest (E_r) and during sessions of activity (E_a):

$$E_m = E_r + E_a \quad (2)$$

For a homeotherm, McNab (1963) described energy expenditure as a function of three variables: time, environmental temperature and rate of metabolism. Energy demand in the individual is a function of the temperature gradient between body temperature (T_B) and ambient temperature (T_A). Heat is lost from the body when $T_A < T_B$ and gained by the body when $T_A > T_B$. The rate of metabolism is inversely proportional to the temperature gradient at temperatures below thermo-

neutrality and directly proportional to temperatures above it. The thermoneutral zone, where metabolism is independent of T_A , is narrow in most desert rodents (Dawson, 1955), sometimes represented by a single point of minimum heat production (Pearson, 1960; Tucker, 1965).

Small rodents, with a relatively large body surface to body weight ratio, gain heat from the environment faster than larger animals. Dissipation of this heat load against a thermal gradient would require evaporative cooling and subsequent water loss — a luxury desert rodents cannot afford. Nocturnalism, torpor, use of burrows and nests, and huddling can mitigate, in part the effects of this physiological stress and modify the subsequent metabolic response. The exigencies of thermoregulation depend on temporal patterning of activity and spatial orientation. Thus, rarely, if ever, do these small, nocturnal animals encounter ambient temperatures that exceed body temperatures. Energy expenditure therefore is concerned primarily with thermogenesis and activity, with additional temporary energy demands during pregnancy and lactation in females.

Seasonal changes in the insulatory properties of the pelage may influence metabolic rates but in small mammals this effect is minimal (Hart, 1956) and has been ignored in this study.

2. DESCRIPTION OF STUDY AREA

The primary study site was in the Hanford Works Department of Energy (DOE) Reservation 19 km northwest of Richland, Benton County, Washington. The 1554 km² reservation, located in the Columbia Basin, has an average basal plain elevation of 150 m. Climatological and edaphic conditions for the general area have been summarized by Stone *et al.* (1972). During the major period of data collection (June 1970—May 1971) 111 mm of rain was recorded, 48 mm less than the long-term average.

Prior to establishment of the reservation in 1943, the general area was used for livestock grazing. Cheatgrass (*Bromus tectorum*), a highly adaptive winter annual, was introduced into eastern Washington about 1890 (Daubenmire, 1970). Overgrazing and fire permitted this annual to replace most of the native species and it is the dominant grass at the Hanford study area. Shrubby species present include big sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and two species of rabbitbrush (*Chrysothamnus nauseosus* and *C. viscidiflorus*). The understory consists of cheatgrass and Sandberg bluegrass (*Poa sandbergii*). Daubenmire (1970) includes the area in the *Artemisia tridentata*-*Poa* association.

3. METHODS

3.1 Microclimate

Temperatures were recorded continuously at the surface and at the average burrow depth (T_b) of 0.5 m by a seven day, two-pen thermograph. Data were

summarized to coincide with the 12 trapping sessions. Mean diurnal surface temperature (T_d) was calculated as the average of even-hour temperatures from dawn to dusk. Correspondingly, mean nocturnal surface temperatures (T_n) were calculated as the average of even-hour temperatures from dusk to dawn. Burrow temperature (T_b) was calculated as the mean of the daily maximum and minimum subsurface temperature.

3.2 Trapping

Rodent populations were sampled monthly using snap-traps spaced approximately 3 m apart, with 50 traps per line. Rolled oats paste was used for bait. Sex weight, position of testes and number of embryos or placental scars were recorded for each individual. Age classes were established by weight and pelage color. All gravid or lactating females were considered adults.

Rodents live-trapped for use in assimilation trials were maintained in laboratory cages on diets including rat chow, rolled oats, sunflower seeds, mixed bird seeds, and occasional »greens«.

3.3 Calorimetry

I determined energy content of materials by combustion in a Parr oxygen bomb calorimeter using standard procedures. When quantity permitted, three replicate samples were burned and the average used as the caloric equivalent. Values were corrected for fuse wire combustion, nitric acid production, and ash

3.4 Seed Production

To obtain an estimate of available seed resources, cheatgrass, the dominant annual and preferred food item for *P. parvus*, was sampled in three consecutive years (1970–72). Collections were made in late May prior to seed fall. Entire cheatgrass plants were harvested on 20 plots (0.1 m²) spaced at 3 m intervals along three parallel transect lines. Seed production was derived from the density-production function of Hulbert (1955, Fig. 15). Average seed weight was determined from seeds removed from cheek pouches of trapped mice. Seed biomass (g/dm²) was calculated as the product of average seed production and the average seed weight.

3.5 Digestibility

The coefficient of digestibility was measured directly in laboratory animals (N=19) and indirectly for animals living in the field (pooled sample, N=30). For direct measurement live-trapped animals were acclimated to captivity for at least 5 days, then fed the test diet for 24 hours prior to trials to insure that the recovered feces represented the test diet. Pre-weighed food (Purina lab chow, rolled oats, or sunflower seeds) was available to test individuals for 3–5 days.

Ingestion was calculated as the difference between initial and final food weights, after correction for changes in water content. Coefficient of digestibility was calculated directly:

$$D_1 = \left(\frac{I-F}{I} \right) \times 100 \quad (3)$$

where *I* is ash-free weight of ingested food and *F* is the ash-free dry weight of resulting feces.

For animals in the wild, living on native foods, an indirect measurement, the ash-tracer technique (Conover, 1966; Johnson & Maxell, 1966), was

used. This method assumes that the animal maintains a mineral balance with ash loss equaling ash intake and that the feces recovered from the rectum are residues of the same dietary constituents as those found in the stomach. Coefficient of digestibility was calculated:

$$D_2 = \left[1 - \frac{(1/y_c) - 1}{(1/y_o) - 1} \right] \times 100 \quad (4)$$

where y_c is the proportion of ash in the feces with a correction for additional ash loss in the urine, and y_o is the proportion of ash in the stomach material. Ash loss in the urine was assumed to be the same as that measured for individuals maintained in the laboratory on a variety of diets.

3.6 Estimation of Individual Energy Expenditure

I calculated ingestion rates by considering the species' activity in field-encountered microclimates (surface and burrows) and the resulting metabolic demands. Adjustments were made for the energy cost of reproduction and for the insulating properties of the nest since both factors influence ingestion rates.

Ingestion rates were calculated using the model:

$$I = \left[(E_r + E_a) + E_{g_3} \right] D^{-1} = (E_m + E_{g_3}) D^{-1} \quad (5)$$

where I is ingestion rate (kcal/yr), E_r and E_a are energy costs while resting and during activity, E_m is their sum (maintenance), E_{g_3} is energy costs for growth from weaning to subadult, and D is coefficient of digestibility. Females incur additional energy demands during pregnancy and lactation as a result from respiration and growth of the embryos. Embryonic respiration has been accounted for by including gravid females in calculations of mean weight. Therefore, ingestion rates for females were calculated as:

$$I_{\varphi} = \left[(E_m + p E_{g_1} + w E_{g_2} + E_{g_3}) \right] (D^{-1}) \quad (6)$$

where p is mean brood size at parturition (i.e., mean litter size \times average number of litters per year), w is the mean brood size at weaning (i.e., mean brood size (p) — mortality during nursing period), and E_{g_1} and E_{g_2} are energy costs for growth from conception to birth and from birth to weaning, respectively. Intrauterine mortality has been ignored.

Mean litter size was based on counts of visible embryos or placental scars. Females with either embryos or placental scars were recorded as bearing one litter: females with both embryos and scars or scars of an undetermined number were recorded as having two litters. Any additional production between the subadult and adult stage is taken into account by using the average adult weight when calculating the energy for maintenance (E_m).

3.7 Energy Costs at Rest and in Torpor

Resting metabolic rates (RMR) and energy demand in torpor (E_t) were taken from the literature. Metabolic rates of animals occupying a nest (E_n) were estimated by adjusting the rate of metabolism at rest as indicated by Pearson (1960).

3.8 Energy Cost of Activity

Since metabolic rate increases during periods of activity, I monitored above-ground activity of free-roaming mice tagged with a radioactive nuclide. Individuals

were live-trapped, anesthetized, and a small length (4–10 mm) of tantalum-182 (half-life 115 days, 1.2 mev) wire implanted subcutaneously in the loose skin between the scapula. Each wire (100–200 μ ci) was encapsulated in catheter tubing.

Tagged individuals were released near their point of capture and their location underground determined by use of a portable Geiger-Muller survey meter (Eberline E-120) equipped with an audio speaker and a modified scintillation probe (Schreiber, 1973). Attempts to monitor above-ground activity of completely free-roaming individuals failed since tagged rodents did not establish »resident« burrows.

To circumvent this problem, two sheet metal enclosures (circumference 15.2 m, area 18.5 m²) buried to a depth of about 30 cm were placed in the field. Plywood nest boxes with plastic tubes opening at the surface were buried in each enclosure. Radionuclide-tagged mice were released in the enclosures and their periods of above-ground activity continuously recorded by a battery operated monitoring device consisting of a NaI gamma scintillation probe, count rate meter and strip chart recorder (Schreiber, 1973). Estimates of daily and seasonal variation in activity were based on these field results, personal communications from other field investigators and published data (French *et al.* 1966).

The amount of energy expended in activity (E_a) is taken from information cited in Chew & Chew (1970).

3.9 Energy Cost of Growth

Energy expended in growth is represented by the general equation:

$$E_g = (WK) (G^{-1}) \quad (7)$$

where E_g is the energy cost for growth during a specific stage of development and each stage of growth is the product of the weight gain (W) and tissue caloric value (K) divided by growth efficiency (G).

4. RESULTS AND DISCUSSION

4.1 Annual Energy Expenditure and Ingestion Rates

Depending on ambient temperature and food availability, *P. parvus* is normally active on the surface from March to October. Metabolic rates for this species have been measured by several investigators (Anderson, 1970; Guthrie, 1972; Meehan, 1975). Guthrie's equations, based on numerous replications, for energy expended during rest (E_r) and torpor (E_t) are:

$$E_r = 8.61 - 0.24 T_b \quad (T_b > 21.3^\circ\text{C}) \quad N=67 \quad (8)$$

$$E_t = 0.38 + 0.01 T_b \quad N=32 \quad (9)$$

where T_b is burrow temperature. An active animal incurs an additional energy loss of about 2.9 ml O₂ ghr⁻¹ (Chew & Chew, 1970). Therefore, energy expended for activity (E_a) is:

$$E_a = 11.51 - 0.24 T_A \quad (10)$$

The insulation of nests afford rodents resting in burrows additional protection against heat loss. Scheffer (1938) found nests for *P. parvus* at depths ranging 86–193 cm. However, in this study, nesting

chambers, found in only 5 of 26 burrow excavations, had an average depth of 48 cm (range 35–61 cm). A well-formed nest, located in chamber $10 \times 10 \times 6$ cm at a depth of 58 cm, weighed 3.5 g and consisted primarily of cheatgrass stems, seed husks and other plant debris. Based on a progressive decrease in the radiation detected, a radionuclide-tagged pocket mouse increased the depth of its resting area as temperatures dropped in the fall. Kenagy (1973) reported similar vertical movement in *Perognathus longimembris*. To account for this behavior, subsurface temperatures taken at 91 cm (Stone *et al.* 1972) were used to calculate metabolic expenditures of torpid and resting animals during the colder months (Fig. 1).

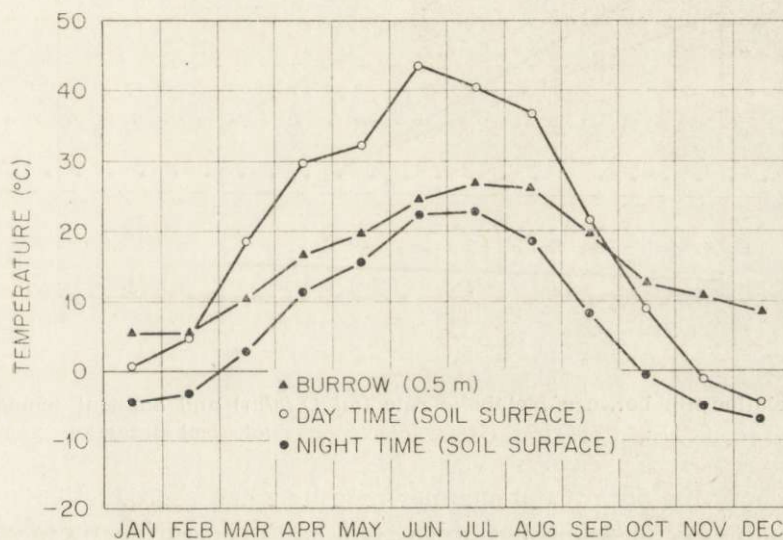


Fig. 1. Microenvironmental temperatures at the Hanford site, June 17, 1970 — June 16, 1971.

Metabolic rate reductions due to the insulating effects of the nest were plotted as $0.81 E_r$ at 1°C and $0.87 E_r$ at 12°C , based on data for a harvest mouse in a natural nest (Pearson, 1960, Fig. 1), and which are comparable to data for *Dipodomys microps* and *Dipodomys merriami* (Kenagy, 1973). The equation fitting the line for energy expended in the nest (E_n) is:

$$E_n = 7.0 - 0.165 T_b \quad (T_b < 21.3^\circ\text{C}) \quad (11)$$

Setting E_n equal to E_r , $T_A = 21.3^\circ\text{C}$. Above this temperature the nest offers no savings in energy (Fig. 2).

To determine requirements for maintenance (E_M), the energy used for

activity (E_a), torpor (E_t) and rest (E_r or E_n) must be quantified in terms of time. Monitoring results in the spring indicate a radionuclide-tagged mouse was active above ground about 5 hours/night, similar to the results reported for *Perognathus formosus* in the Mohave desert (French, et al., 1966). This amount of activity would presumably

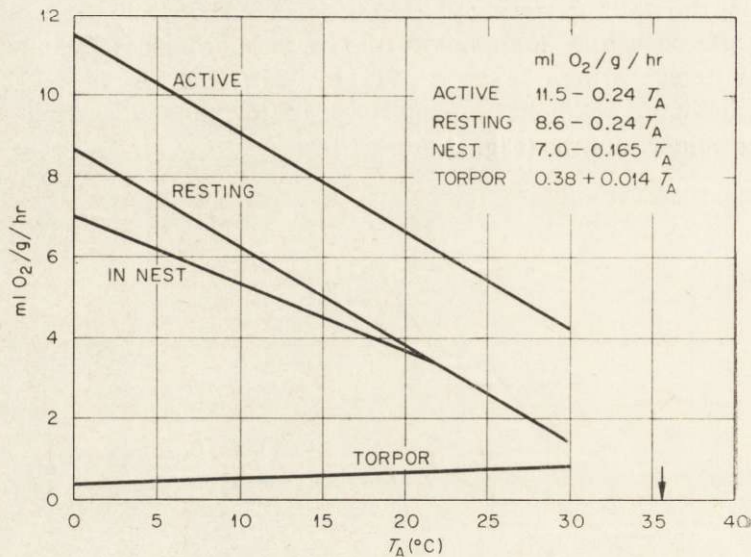


Fig. 2. Relationship between metabolic rate (ml O₂/g/hr) and ambient temperature (T_A) in *P. parvus* during selected physiological states.

apply to both the spring and summer months when reproductive activity and foraging are at a peak. Ambient temperatures during these seasons exact minimum energy costs for thermoregulation in *P. parvus*.

Based on trapping success (Schreiber, 1973), activity is greatly reduced in the fall prior to torpor and during the cooler part of early spring. Males are active later in the fall and earlier in the spring than females. I estimated the activity time during these transition periods (Tables 1 and 2).

Based on field recordings animals were seldom exposed to burrow temperatures below 5°C (Fig. 1). Since this species accumulates no appreciable body fat, their overwinter survival depends on food caches and periodic torpor (Schreiber & Johnson, 1975). Although heteromyids are highly individualistic in their proclivity for torpor, the pattern and periodicity is apparently a function of the amount of food stored and environmental conditions of the habitat (Brown & Bartholomew, 1969; Tucker, 1966; Meehan, 1975). During

the coldest part of the year (mid-November to mid-March) the above-ground activity of this species is severely curtailed or absent. In years with high populations and late litters, subadults may be active into

Table 1.

Estimated daily activity and annual maintenance energy expenditure for a male *Perognathus parvus*.

Time Interval		Body Wt. (g)	Hours Daily			Metabolic Costs (kcal) ^a			
Dates	Days		At Rest	In Torpor	Active	E_r	E_t	E_a	E_m
6/17—6/28	12	19.17	16	3	5	49.5	2.3	33.7	85.5
6/29—8/3	36	18.31	16	3	5	110.4	6.4	96.5	213.3
8/4—9/10	38	16.26	16	3	5	111.5	6.7	105.3	223.5
9/11—10/12	32	16.42	11	11	2	105.4	18.0	48.4	171.8
10/13—11/15	34	15.52	12.5	11	0.5	155.1	15.3	14.9	185.3
11/16—12/5	20	16.19 ^b	4	20	0	32.6	15.5	0	48.1
12/6—1/1	27	16.85 ^b	4	20	0	48.9	21.4	0	70.3
1/2—2/4	34	17.52 ^b	4	20	0	69.8	24.6	0	94.4
2/5—3/12	36	18.19 ^b	3.5	20	0.5	67.1	28.3	19.5	114.9
3/13—4/11	30	18.85	11	11	2	159.7	14.9	59.4	234.0
4/12—5/11	30	19.62	8	11	5	96.5	18.6	125.7	240.8
5/12—6/16	36	19.02	16	3	5	194.6	6.4	127.4	328.4
Annual Total (kcal/yr) with summer torpor						1201.1	178.4	630.8	2010.3
						(59.7)	(8.9)	(31.4)	
without summer torpor						1286.4	153.0	630.8	2070.2
						(62.1)	(7.4)	(31.4)	

^a Based on microenvironmental temperatures (Fig. 1).

^b Estimated body weight used a constant proportion of the known average weight gain over winter.

December and January (O'Farrell, *et al.*, 1975). However, this deviation in seasonal activity is apparently related to above-average winter annual vegetation production and has therefore been ignored when calculating average energy requirements for the species.

Torpor bouts in *P. parvus* may last from 3—240 hours (Iverson, 1967; Hayden & Lindberg, 1970; Meehan, 1975). During the coldest months they spend about 60—80% of their time in torpor (Chew *et al.*, 1965; Iverson, 1967) so an estimate of 20 hours torpor daily was used to calculate average winter energy costs.

During the early fall and early spring, torpor permits metabolic savings between the intermittent periods of surface activity and resting in the nest. Tucker (1962) reported diurnal torpor in *Perognathus californicus* at 15°C, even with free access to food. At this temperature with moderate food rations, this species averaged 11 hours (range 7—15) in torpor (Tucker, 1966). *Perognathus formosus* at 17°C spent about 10 hours/day in torpor (Brower & Cade, 1971). I used 11 hours of

torpor to calculate metabolic costs in *P. parvus* during the spring and fall.

It is unknown if *P. parvus* exhibits summer torpor (estivation) under natural conditions. In summer when food is more available and burrow temperatures are high, torpor might seem less advantageous. However, it may serve as an important means of conserving body water and

Table 2

Estimated daily activity and annual maintenance energy expenditure for a female *Perognathus parvus* at the Hanford site.

Time Interval		Body Wt. (g)	Hours Daily			Metabolic Costs (kcal) ^a			
Dates	Days		At Rest	In Torpor	Active	E_r	E_t	E_a	E_m
6/17—6/28	12	17.47	16	3	5	45.1	2.2	30.7	78.0
6/29—8/3	36	16.92	16	3	5	100.6	6.6	89.2	196.4
8/4—9/10	38	16.70	16	3	5	114.5	6.8	108.1	229.4
9/11—10/12	32	17.36	12	11	1	121.6	19.1	25.5	166.2
10/13—11/15	34	16.66 ^b	12.5	11	0.5	166.5	16.4	16.0	193.9
11/16—12/5	20	15.96 ^b	4	20	0	29.4	23.0	0	52.4
12/6—1/1	27	15.26 ^b	4	20	0	44.3	10.8	0	64.1
1/2—2/4	34	14.56 ^b	4	20	0	58.0	21.4	0	79.4
2/5—3/12	36	13.86 ^b	4	20	0	58.4	21.6	0	80.0
3/13—4/11	30	13.16	12	11	1	121.7	10.4	20.6	152.7
4/12—5/11	30	15.31	8	11	5	75.7	14.6	98.1	183.4
5/12—6/16	36	16.67	16	3	5	170.5	5.6	111.6	287.7
Annual Total (kcal/yr) with summer torpor						1106.3	167.5	499.8	1773.6
						(62.4)	(9.4)	(28.2)	
without summer torpor						1186.8	146.3	499.8	1832.9
						(64.7)	(8.0)	(28.2)	

^a Based on microenvironmental temperatures (Fig. 1).

^b Estimated body weight based a constant proportion of the known average weight gain over winter.

energy between periods of reproductive activity and foraging. Circumstantial evidence indicates a tendency for at least periodic bouts of summer torpor in this genus. For example, Meehan (1975) reported *P. parvus* in the laboratory entered torpor spontaneously in the presence of hoarded food at 18 and 6°C during both summer and winter. Iverson (1967) found torpid *P. parvus* in live traps from April to November and reported spontaneous torpor (in the presence of food) occurred in the laboratory at temperatures up to 20°C. Others (e.g., Bartholomew & Cade, 1957; Bartholomew & MacMillen, 1961) have found heteromyids are easily induced into torpor at temperatures from 5—22°C when starved. Cade (1964), in his discussion of the evolution of torpidity in rodents, states 12 species of *Perognathus* exhibit varying degrees of torpor at temperatures 5—25°C.

Periodic bouts of summer torpor for *P. parvus* have been suggested by O'Farrell *et al.* (1975). At ambient temperature 24°C and with food, Chew *et al.* (1965) found the little pocket mouse, *Perognathus longimembris*, was hypometabolic 12.5% of the time. However, French (1976) studying hibernation in this species concluded it probably does not become torpid during the summer months since it selects the most advantageous (highest) subsurface temperatures available during the year and that torpor would occur only when this temperature is significantly below minimum (lower critical) temperature of thermal neutrality. For purposes of comparison, summer metabolic requirements were calculated both with and without the possible savings of torpor. Based on the data of Chew *et al.* (1965) I assumed 3 hours of daily torpor, as might occur during summers with low cheatgrass production (food restriction) and/or extreme microclimate conditions (thermal stress, dehydration).

Pocket mice are solitary animals and it is doubtful whether individuals huddle during cold weather. Pairs housed together in the laboratory were pugnacious and one usually died. Often the dead animal showed little or no sign of physical injury, suggesting death may have been caused by stress. In the field Scheffer (1938) never found more than a single mouse using a winter nest. Therefore, it is unlikely huddling is a significant method of reducing thermoregulatory costs in *P. parvus*.

Estimates of the annual costs for maintenance (E_m) in male and female pocket mice are given in Tables 1 and 2. To calculate the individual's annual ingestion rate, the additional energy expenditure for growth is needed. For the male it includes only growth after weaning (Eq. 6). For the females however this energy cost must also include the expense of bearing and raising young (Eq. 7).

Weight gains (W) were determined for each growth stage. The average weight of *P. parvus* born in the laboratory was 1.27 g ($N=5$), approximating the greatest weight of an embryo found *in utero*. Weight of embryonic tissues increases this 27% (Kaczmarek, 1966). Weaning weight was considered 6.4 g, the weight of the smallest pocket mouse captured. Subadult weights for males and non-gravid females were 13.0 and 11.5 g, respectively. I used the following caloric values for the tissues (K): for the embryo, 0.98 kcal/g fresh weight, based on the average caloric values of five species of newborn rodents (Górecki, 1965; Myrcha & Walkowa, 1968; Sohlt, 1973); for the unweaned young, 1.39 kcal/g, assuming an average weaning age of 25 days and the mean caloric value of two species of rodents (Myrcha & Walkowa, 1968; Sohlt, 1973), and for weaned young, 1.55

kcal/g (Schreiber & Johnson, 1975). Lacking specific data for growth efficiency (G) during gestation and lactation, I used that calculated by Kaczmariski (1966) for the bank vole (*Clethrionomys glareolus*) and by Migula (1969) for the common vole (*Microtus arvalis*). Based on the average of these values, $G=13.8\%$ for embryos and 15.0% for unweaned young. The efficiency of growth in weaned young was assumed equal to efficiencies determined for the common vole from weaning up to the age of 50 days (Drozd *et al.* 1972), *i.e.*, $G=5.0\%$.

The cost for growth from weaning to subadult was calculated as:

$$E_{g3} = (WK)(G^{-1})$$

$$\sigma = (6.6)(1.55)/0.05 = 204.6 \text{ kcal} \quad (12)$$

$$\varphi = (5.1)(1.55)/0.05 = 158.1 \text{ kcal} \quad (13)$$

Using a coefficient of digestibility of 89.2% , based on animals living in the wild on natural diets, the annual ingestion rate for an individual male was calculated (Eq. 6):

$$I\sigma = (2010 + 205)/0.892 = 2483 \text{ kcal/yr (with summer torpor)} \quad (14)$$

$$\text{or} = (2070 + 205)/0.892 = 2550 \text{ kcal/yr (without summer torpor)} \quad (15)$$

Females have an additional energy increment for producing young. Mean litter size for *P. parvus* at the Hanford site in 1970–1971 was 3.9 ($N=82$). This is smaller than values reported for this species in southern British Columbia (4.8, Iverson, 1967), southeastern Washington (5.2, Scheffer, 1938), Utah (5.4, Duke, 1957) and Nevada (5.6, Hall, 1946). Females normally raise 1–2 litters per year. During this study the average number of litters per year was 1.10 ($N=57$). I have assumed a conservative survival rate of 80% for nursing young (Kaczmariski, 1966). The coefficient of digestibility of females was 91.1% . Annual ingestion rate for an individual female was calculated as:

$$I\varphi = (E_m + pE_{g1} + wE_{g2} + E_{g3})(D^{-1})$$

$$= (1774 + 49 + 153 + 158)/0.911 = 2342 \text{ kcal/yr (with summer torpor)} \quad (16)$$

$$= (1883 + 360)/0.911 = 2462 \text{ kcal/yr (without summer torpor)} \quad (17)$$

Of the total energy expended in growth (E_g), an individual animal used 13.6% from conception to birth, 42.5% from birth to weaning and 43.9% from weaning to subadult.

From the energy required annually for maintenance, *P. parvus* spent approximately $60\text{--}65\%$ during rest, $7\text{--}9\%$ in torpor and $27\text{--}31\%$ in activity (Tables 1 and 2). Summer torpor would permit an annual energy savings of about 3% . Because of extensive torpor, daily energy expenditure in the winter is estimated as only $40\text{--}43\%$ of that required in the summer.

4.2 Ecological Implications

Cheatgrass seeds formed a major portion of the pocket mouse's diet at the Hanford site (Schreiber, 1973). The productivity of such winter annuals fluctuates greatly from year to year, apparently in response to the time and amount of precipitation (Sneva, 1965; Beatley, 1967, 1969). Cheatgrass seed production during three grow-

Table 3
Annual cheatgrass production at the Hanford study sites, 1970—1972.

Year	Site	Density (plants/0.1 m ² ±SE)	Culms (culms/0.1 m ² ±SE)	Seed density ^a (no./dm ²)	Biomass ^b (k/ha)	Caloric ^c value (Mcal/ha)
1970	Arc 6	94.2±13.1	96.9±13.1	18	30.5	140
1971	B-27	38.4± 3.7	39.3± 3.9	24	40.7	187
1972	B-27	30.0± 4.7	33.4± 4.6	26	44.1	203
Mean		54.2± 4.7	56.5± 4.8	22.6	38.4	177

^a Hulbert (Fig. 15, 1955).

^b Based on average of 590 seeds/gram.

^c Caloric value of cheatgrass seeds is 4.61 kcal/g (Schreiber, 1973).

Table 4
Estimated daily maintenance energy requirements and food consumption in adult *Perognathus parvus* at the Hanford site.

Time interval	Length (days)	Mean body weight (g)	Energy requirements				Daily seed consumption ^b	
			kcal/day	Percent BMR (% ₀) ^a	kcal/g	kcal/g/hr	g ^c	No. ^d
Male								
2/5—6/16	132	18.9	6.96	195	0.368	0.015	1.69	999
6/17—9/10	86	17.9	6.07	178	0.339	0.014	1.48	873
9/17—11/15	66	16.0	5.41	172	0.338	0.014	1.32	776
11/16—2/4	81	16.8	2.63	83	0.156	0.006	0.64	379
Female								
3/13—6/16	96	15.0	6.55	218	0.437	0.018	1.55	920
6/17—9/10	86	17.0	5.86	182	0.405	0.017	1.64	969
9/11—11/15	66	17.0	5.53	166	0.325	0.014	1.32	777
11/16—3/12	117	14.9	2.36	80	0.158	0.006	0.56	332

^a Basal metabolic rate (BMR)=70 W^{0.75}, W=body weight (kg) (Kleiber, 1961).

^b Digestibility coefficients; male = 0.892, female = 0.911.

^c Based on 4.61 kcal/gram of cheatgrass seeds.

^d Based on 590 seeds/gram, 1 seed = 1.69 mg.

ing seasons averaged 38 kg/ha or 177 Mcal (Table 3). Assuming a diet consisting entirely of cheatgrass seeds, the estimated daily seed consumption by adult *P. parvus* at the Hanford site is given in Table 4.

These values indicate pocket mice consume about 4–10% of their body weight in food per day for maintenance. Summer values are comparable to the daily consumption values Anderson (1970) gave for *P. parvus* at 20–30°C. Based on my torpor estimates, seed caches of about 46 g for males and 60 g for females would be required to insure overwinter survival. Stored seeds probably amount to 60–70 g based on the reported volume of excavated caches (Scheffer, 1938; Iverson, 1967).

Using these calculations, an individual pocket mouse would require about 262,000 to 289,000 cheatgrass seeds per year. Given that I have reasonably estimated periods of daily activity in this species (*i.e.*, 839–919 hrs/yr), an individual would need to collect about 300 seeds per hour of surface activity to satisfy the predicated maintenance energy demands.

In the semi-arid lowlands of southern British Columbia Iverson (1967) found *P. parvus* had a home range of 656–895 m². O'Farrell *et al.* (1975), studying populations at somewhat higher elevations on the Hanford Reservation, calculated an average home range of 2140 m² for adults. Assuming these estimates of home range size are valid for my study area and given the average seed deposition rate of 2260/m² (Table 3), then there are approximately 1.5–2.0 × 10⁶ cheatgrass seeds potentially available to an individual within its area of normal activity, or between 5 to 8 times its predicted annual energy requirements.

There is some evidence however that this species is periodically resource stressed. Densities during peak years may exceed 100/ha (O'Farrell *et al.*, 1975); in fact, results from snap-trapping in my study area suggested populations may exceed 180/ha (Schreiber, 1973). Data from O'Farrell *et al.* (1975) indicates an inverse relationship between population density and home range size. Their data suggest that at densities greater than 100/ha the home range may actually be less than 500 m². Even with smaller home range sizes these densities would require considerable overlap and competition for the available seeds. With an average seed crop and a conservative estimate of 50–95% seed recovery (Odum *et al.*, 1962; Chew & Chew, 1970; Soholt, 1973), the maximum sustainable population would range between 39–83 animals/ha. Although this species consumes other types of seeds, plant parts, and even insects (particularly in the spring), one would expect substantial mortality before the next breeding season whenever populations exceed about 80/ha.

Recently, Reichman (1977a) presented evidence that in the southern deserts there is considerable competition between heteromyids and ants. If similar circumstances exist in the northern cold deserts, my

estimates of maximum sustainable populations would require reduction. Birds appear less specific in their use of cheatgrass seeds (Goebel & Berry, 1976) and are probably less competitive with *P. parvus*. Interestingly, at the Hanford site there are presently no other heteromyids and this lack of interspecific competition common to its southern counterparts may permit comparatively higher densities during years of high cheatgrass production.

Reichman (1977b) suggested heteromyids reduce the number of seeds required to meet their energy demands by selecting seed species that are energetically appropriate. In the case of *P. parvus*, annual grass seeds (~ 4.6 kcal/g) represent the most available seed source (Kritzman, 1974; Schreiber, 1973), although certain high energy seeds, such as *Salsola iberica* (5.7 kcal/g), may be seasonally important in their diet. It has been shown that heteromyids may exert considerable influence on certain plant species by their preferential seed predation and browsing (e.g., Soholt, 1973; Meehan *et al.*, 1977) which in turn could affect plant succession. At Hanford, the extensive use of cheatgrass seeds implies such potential. Obviously some seeds escape detection and many surface caches may not be relocated. When a large percentage of these seeds are removed however, germinating plants have less competition for soil nutrients and moisture and respond with greater seed production (Hulbert, 1955). Therefore the total effect of *P. parvus* on cheatgrass abundance is probably small. The major forcing function directing the system probably lies instead in the pattern and amount of annual precipitation (e.g., Beatley, 1969; O'Farrell *et al.*, 1975). To exploit a food source that demonstrates oscillating annual differences in yield and comprises only about 7% of the vegetation production, *P. parvus* must therefore, (1) be highly efficient in collecting seeds and in assimilating their energy, and (2) rely on the use of facultative torpor throughout the year to balance the residual energy demands.

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REFERENCES

1. Anderson S. H., 1970: Effect of temperature on water loss and CO₂ production of *Perognathus parvus*. *J. Mammal.*, 51: 619—620.
2. Bartholomew G. A., & Cade T. J., 1957: Temperature regulation, hibernation, and aestivation in the little pocket mouse, *Perognathus longimembris*. *J. Mammal.*, 38: 60—72.
3. Bartholomew G. A. & MacMillen R. E., 1961: Oxygen consumption, estivation and hibernation in the Kangaroo mouse, *Microdipodops pallidus*. *Physiol. Zool.*, 34: 171—178.
4. Beatley J. C., 1967: Survival of winter annuals in the northern Mojave Desert. *Ecology*, 48: 745—750.
5. Beatley J. C., 1969: Dependence of desert rodents on winter annuals and precipitation. *Ecology*, 50: 721—724.
6. Brower J. E. & Cade T. J., 1971: Bircadian torpor in pocket mice. *BioScience*, 21: 181—182.
7. Brown J. H. & Bartholomew G. W., 1969: Periodicity and energetics of torpor in the kangaroo mouse, *Microdipodops pallidus*, *Ecology*, 50: 705—709.
8. Cade T. J., 1964: The evolution of torpidity in rodents. *Ann. Acad. Sci. Fenn.*, IV Biol., 71 (6): 79—112.
9. Chew R. M. & Chew A. E., 1965: The primary productivity of a desert shrub (*Larrea tridentata*) community. *Ecol. Monogr.*, 35: 355—375.
10. Chew R. M. & Chew A. E., 1970: Energy relationships of the mammals of a desert shrub (*Larrea tridentata*) community. *Ecol. Monogr.*, 40: 1—21.
11. Chew R. M., Lindberg R. G. & Hayden P., 1965: Circadian rhythm of metabolic rate in pocket mice. *J. Mammal.*, 46: 477—494.
12. Conover R. J., 1966: Assimilation of organic matter by zooplankton. *Limnol. Oceanogr.* 11: 338—345.
13. Daubenmire R., 1970: Steppe vegetation of Washington. Washington State Agri. Exp. Sta. Tech. Bull. 62, Coll. of Agri., Washington State Univ. 131 p.
14. Dawson W. R., 1955: The relation of oxygen consumption to temperature in desert rodents. *J. Mammal.*, 36: 543—553.
15. Drożdż A., Górecki A. & Sawicka-Kapusta K., 1972: Bioenergetics of growth in common voles. *Acta theriol.*, 18: 245—257.
16. Duke K. L., 1957: Reproduction in *Perognathus*. *J. Mammal.*, 38: 207—210.
17. French A. R., 1976: Selection of high temperatures for hibernation by the pocket mouse, *Perognathus longimembris*: ecological advantages and energetic consequences. *Ecology*, 57: 185—191.
18. French N. R., Maza B. G. & Aschwanden A. P., 1966: Periodicity of desert rodent activity. *Science*, 154: 1194—1195.
19. Goebel C. J. & Berry G. 1976: Selectivity of range grass seeds by local birds. *J. Range Manage.*, 29: 393—395.
20. Górecki A., 1965: Energy values of body in small mammals. *Acta theriol.*, 10: 333—352.
21. Guthrie D. R., 1972: The effect of torpor on pulmo-cutaneous water loss in *Perognathus parvus*. Ph. D. dissertation, Univ. British Columbia, Vancouver. 81 p.

22. Hall E. R., 1946: Mammals of Nevada. Univ. California Press: 1—710. Berkeley.
23. Hart J. S., 1956: Seasonal changes in insulation of the fur. Canadian J. Zool., 34: 53—57.
24. Hayden P. & Lindberg R. G., 1970: Hypoxia-induced torpor in pocket mice (Genus: *Perognathus*). Comp. Biochem. Physiol., 33: 167—179.
25. Hulbert L. C., 1955: Ecological studies of *Bromus tectorum* and other annual brome grasses. Ecol. Monogr., 25: 181—213.
26. Iverson S. L., 1967: Adaptations to arid environments in *Perognathus parvus* (Peale). Ph.D. Dissertation, Univ. British Columbia. 130 p.
27. Johnson D. R. & Maxell M. H., 1966: Energy dynamics of Colorado pikas. Ecology, 47: 1057—1061.
28. Kaczmarzski F., 1966: Bioenergetics of pregnancy and lactation in the bank vole. Acta theriol., 11: 409—417.
29. Kenagy G. J., 1973: Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. Ecology, 54: 1201—1219.
30. Kleiber M., 1961: The Fire of Life. John Wiley & Sons, Inc: 1—454. New York.
31. Kritzman E. B., 1974: Ecological relationship of *Peromyscus maniculatus* and *Perognathus parvus* in eastern Washington. J. Mammal., 55: 172—188.
32. McNab B. K., 1963: A model of the energy budget of a wild mouse. Ecology, 44: 521—532.
33. Meehan T., 1975: Profound spontaneous torpor in *Perognathus parvus*. Amer. Soc. Mammalogists 55th Ann. Mtg. (Abstr.), Univ. Montana, Missoula.
34. Meehan T., Rundel P. W., Ambrose R., Baker G. & Rappaport A., 1977: The influence of intense selective browsing by pocket mice (*Perognathus*) on the spatial distribution of *Polygala deserticum* in Baja California. Amer. Midl. Nat., 97: 489—495.
35. Migula P., 1969: Bioenergetics of pregnancy and lactation in European common vole. Acta theriol., 14: 167—179.
36. Myrcha A. & Walkowa W., 1968: Changes of the caloric value of the body during the postnatal growth development of white mice. Acta theriol., 13: 391—400.
37. Odum E. P., Connell C. E. & Davenport L. B., 1962: Population energy flow of three primary consumer components of old-field ecosystems. Ecology, 43: 88—96.
38. O'Farrell T. P., Olson R. J., Gilbert R. O. & Hedlund J. D., 1975: A population of Great Basin pocket mice, *Perognathus parvus*, in the shrub-steppe of southcentral Washington. Ecol. Monog., 45: 1—28.
39. Pearson O. P., 1960: The oxygen consumption and bioenergetics of harvest mice. Physiol. Zool., 33: 152—160.
40. Petrusewicz K. (ed.), 1967: Secondary productivity of terrestrial ecosystems (Principles and Methods). Państw. Wyd. Nauk.: 1: 1—379. Warszawa.
41. Petrusewicz K. & Macfadyen A. (ed.), 1970: Productivity of terrestrial animals, principles and methods. IBP Handbook No. 13. F. A. Davis, Co: 1—190. Philadelphia, Pennsylvania.
42. Petrusewicz K. & Ryszkowski L. (ed.), 1969: Energy flow through small mammal populations. Państw. Wyd. Nauk.: 1—298. Warszawa.

43. Reichman O. J., 1977a: Field experiments on seed use by desert rodents and ants. Amer. Soc. Mammalogists 57th Ann. Mtg. (Abstr.), Michigan State Univ., East Lansing.
44. Reichman O. J., 1977b: Optimization of diets through food preferences by heteromyid rodents. Ecology, 58: 454—457.
45. Scheffer T. H., 1938: Pocket mice in Washington and Oregon in relation to agriculture. U. S. Dept. Agr. Tech. Bull. No. 608: 1—15.
46. Schreiber R. K., 1973: Bioenergetics of rodents in the northern Great Basin desert. Ph.D. dissertation, Univ. Idaho, Moscow. 133 p.
47. Schreiber R. K. & Johnson D. R., 1975: Seasonal changes in body composition and caloric content of Great Basin rodents. Acta theriol., 20: 343—364.
48. Sneva F. A., 1965: Cheatgrass yields and precipitation fluctuations, p. 27—29. Proc. Cheatgrass Symp., July 27—30, 1965. U.S. Dept. of Interior, BLM, Oregon-Washington State Office. 92 p.
49. Scholt L. F., 1973: Consumption of primary productivity by a population of kangaroo rats (*Dipodomys merriami*) in the Mojave Desert. Ecol. Monog., 43: 357—376.
50. Stone W. A., Jenne D. E. & Thorp J. M., 1972: Climatology of the Hanford Area. BNWL-1605, June 1971 Battelle Pacific Northwest Lab., Richland, Washington.
51. Tucker V. A., 1962: Diurnal torpidity in the California pocket mouse. Science, 136: 380—381.
52. Tucker V., A., 1965: Oxygen consumption, thermal conductance, and torpor in the California pocket mouse, *Perognathus californicus*. J. Cell. Comp. Physiol., 65: 393—404.
53. Tucker V. A., 1966: Diurnal torpor and its relation to food consumption and weight changes in the California pocket mouse *Perognathus californicus*. Ecology, 47: 245—252.

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BIOENERGETYKA *PEROGNATHUS PARVUS*

Streszczenie

U *Perognathus parvus*, odławianych w południowo-centralnym Waszyngtonie (rezerwat Hanford) zmierzono zużycie pokarmu i roczne wydatki energetyczne. Zużycie pokarmu badano w zależności od czasu, tempa metabolizmu, temperatur mikrośrodowiska i współczynnika strawności (Ryc. 1 i 2). Oszacowane w ten sposób zapotrzebowanie pokarmowe jest równe 2550 i 2462 kcal/rok odpowiednio dla samicy i samca. W lecie, dzięki okresowym odrętwieniom, koszt energetyczny zmniejsza się o około 3%. Zimą, kiedy okresy odrętwienia są wydłużone, wydatki energetyczne są o 40—43% niższe niż latem (Tabela 1 i 2). Dobowy koszt energetyczny zwierząt zimujących jest najniższy i wynosi 2,36 kcal/samica i 2,63 kcal/samica. Najwyższy zaś jest na wiosnę osiągając odpowiednio dla dorosłej samicy i samca wartości 6,96 i 6,55 kcal (Tabela 4), co świadczy, iż *P. parvus* konsumuje dziennie pokarm stanowiący 4—10% ciężaru swego ciała. Przeliczając te ilości na pokarm

złożony wyłącznie z nasion *Bromus tectorum* wykazano, iż jeden osobnik potrzebuje 873—999 nasion/dobę wiosną i latem i około 775 nasion jesienią. W zimie, dzięki fakultatywnemu odrętwieniu ilość ta zmniejsza się do około 400 (Tabela 4).

Zbadano również produkcję nasion *Bromus tectorum* (Tabela 3) i obliczono, że średni roczny plon nasion tej trawy umożliwia wyżywienie dla maksymalnie 80 osobników/ha. Ponieważ w latach szczytu liczebności zagęszczenie badanego gatunku jest większe może mieć tu miejsce stress pokarmowy. Przypuszcza się, że rzeczywista presja *P. parvus* na sukcesję traw jest mniejsza niż wynika to z prezentowanych wyliczeń.