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ANNUAL ENERGY BUDGETS FOR THREE COMMON RODENT SPECIES IN THE NORTHERN GREAT BASIN[1]

R. Kent Schreiber[2,3]

Abstract.— Annual energy budgets were calculated for three species of small mammals (*Peromyscus maniculatus, Onychomys leucogaster, Reithrodontomys megalotis*) from the northern Great Basin, Benton County, Washington. Individual ingestion rates were based on species activity, microclimate regime, coefficient of digestibility, caloric diet, and the cost for reproduction. For males and females, the estimated energy expenditures were: *P. maniculatus*, 6080, 5891; *O. leucogaster*, 5714, 6587; and *R. megalotis*, 4057, 3791 kcal/yr. By comparison, each species on an individual basis processes more energy annually than the more abundant species in the community, *Perognathus parvus*, but their total contribution to community energy flow is apparently minor. Integration of these results with other ecological parameters is necessary to develop new hypotheses on the role of small mammal consumers in cold desert ecosystems.

Historically, ecologists have studied and compared ecosystems and their component species in terms of density and biomass. However, this approach does not emphasize the impact of each species on the total system or its relationship to other trophic levels within the system. The concept of energy flow provides such a common factor for comparing ecosystems and also for evaluating the relative importance and success of the constituent populations.

In the northern part of the Great Basin common rodent species include the Great Basin pocket mouse (*Perognathus parvus*), deer mouse (*Peromyscus maniculatus*), northern grasshopper mouse (*Onychomys leucogaster*) and the western harvest mouse (*Reithrodontomys megalotis*). These small mammal consumers are representative of an important pathway for energy transfer in a cold desert ecosystem. The bioenergetics of the predominant species, *P. parvus*, has been discussed in a previous paper (Schreiber 1978b). This paper reports on the energy budgets of the three, less abundant, species.

Energy flow through a rodent population can be determined from daily energy requirements and ingestion rates of individuals during each season. In this study I calculated ingestion rates by considering activity of each species in field-encountered microclimates and their resulting metabolic demands. Adjustments in the ingestion rates were made for the additional energy cost of reproduction and for the energy savings while residing in a nest.

Materials and Methods

Study Area

The study area is in the Hanford Works Department of Energy (DOE) Reservation 19 km northwest of Richland, Benton County, Washington. The 58-year average annual precipitation for the Reservation is 159 mm. Other climatological and edaphic conditions for the general area have been summarized by Stone, Jenne, and Thorp (1972). Vegetation is mostly typical of the *Artemisia tridentata-Poa* association (Daubenmire 1970) with the exception of native grass species. Cheatgrass (*Bromus tectorum*) was introduced into the area over a half century ago and now has replaced native species as the dominant ground cover. Shrubby species present include big sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and two rabbitbrush species (*Chrysothamnus nauseosus*; *C. viscidiflorus*).

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Trapping

Although no attempt was made in this study to delineate absolute population numbers, monthly sampling with snap-traps determined species composition, relative population sizes, and trends. Traps were spaced approximately 3 m apart, with 50 traps per 150 m line. Rolled oats paste was used for bait and traps were normally set for three consecutive nights in each trapping session. Sex, weight, and reproductive status of all captures were recorded. In addition, rodents were live-trapped in peripheral areas for use in laboratory food trials.

Microclimate

To establish the microclimate regime of the species, temperatures were recorded continuously at the surface and at a burrow depth of 0.5 m by a seven-day, two-pen thermograph. Data were summarized to coincide with monthly 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.

Digestibility

Energy content of ingested materials was determined by combustion in a semimicro oxygen bomb calorimeter. The coefficient of digestibility (digested proportion of ingested food) was measured directly in the laboratory from food intake and indirectly by the ash-tracer method for free-living animals (Schreiber 1979).

Energy Expenditure

Annual ingestion rates were calculated from the activity and resting time of the species in field-encountered microclimates (surface and burrows) and their resulting caloric demands. The additional energy cost of reproduction and the energy savings from insulating properties of the nest were incorporated into the calculations.

Ingestion rates were calculated using the general model:

$$I = [(E_r + E_a) + E_{g_3}]\, D^{-1}$$
$$= (E_m + E_{g_3}) D^{-1} \qquad (1)$$

where I is ingestion rate (kcal/yr), E_r and E_a are energy costs during rest 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. Additional growth between the subadult and adult stage was considered by using the average adult weight when calculating maintenance energy (E_m). During pregnancy and lactation, females incur additional energy demands due to respiration and growth of the embryos. To account for embryonic respiration, gravid females were included in calculations of female mean weight. Ingestion rates for females were calculated as—

$$I_f = (E_m + p\, E_{g_1} + w\, E_{g_2} + E_{g_3})\, (D^{-1}) \qquad (2)$$

—where the coefficient p is mean brood size at parturition (i.e., mean litter size × average number of litters per year), w is the mean brood size at weaning (i.e., mean brood size (p) minus 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 is unknown but probably small and has been ignored in the calculations. 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. For all species I assumed a conservative survival rate of 80 percent for nursing young (Kaczmarski 1966).

Energy Costs at Rest: Resting metabolic rates (RMR) for individual species were taken from the literature. Since animals in a burrow and occupying a nest have lower energy requirements during rest, I adjusted RMR's for this energy conservation by plotting the nesting metabolic rate (NMR) as a regression line based on 0.81 RMR at 1 C and 0.87 RMR at 12 C (based on data reported for the harvest mouse, Pearson 1960).

Energy Cost of Activity: Metabolic rates increase during periods of activity. Estimates of daily and seasonal variations in amounts of activity were based on field-monitored activity of free-roaming mice tagged with a radioactive nuclide (Schreiber 1973), personal communications from other field investigators, and published data (French et al., 1966). The incremental energy demand (E_a) during these activity period was calculated from information cited in Chew and Chew (1970).

Energy Cost of Growth: Energy cost for growth during a specific stage of development (E_g) is the product of the weight gain (W) and tissue caloric value (K) divided by growth efficiency (G) during that period of growth, i.e.,

$$E_g = (WK)(G^{-1}) \quad (3)$$

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 (Gorecki 1965, Myrcha and Walkowa 1968, Soholt 1973), and 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 and Walkowa 1968, Soholt 1973). Caloric values for weaned young of individual species are given in the results. Growth efficiencies were taken from the literature and based on average values, G = 13.8 percent for embryos, 15.0 percent for unweaned young, and 5.0 percent for weaned young (Kaczmarski 1966, Migula 1969, Drozdz et al. 1972).

RESULTS AND DISCUSSION

Composition and Abundance

Snap traps effectively sample small mammal populations (Wiener and Smith 1972), and they are particularly applicable for censusing large areas. Under ideal conditions the total number of individuals caught in traps is proportional to population density and reflects the structure of the population (Hansson 1967, Petticrew and Sadlier 1970). Although trapping percentages are not direct estimates of density, they are nonetheless indicative of population trends and therefore provide insight into the influence a particular species has in the transfer of energy into the community.

Trap lines were operated one night each in September and November 1969 and March, April, and May 1970 and at least three nights per month from June 1970 to May 1971 (Table 1). A total of 1470 rodents was captured in 14,289 trap-days (one trap set for one day). The average monthly effort was 794 trap-days and the overall trapping success was 10.3 percent. Field observations indicated traps placed in dense cover or concealed by shadows had somewhat greater success. On other areas of the Hanford Reservation general trapping success has been reported as low as 4 percent on fire-disturbed grasslands with stony soils (Hedlund et al. 1975) and as high as 44 percent in shrub-steppe habitats with coarse-textured sands (O'Farrell 1975b).

A total of four species of rodents was snap-trapped on the study area: the Great Basin pocket mouse, *Perognathus parvus*; deer mouse, *Peromyscus maniculatus*; northern grasshopper mouse, *Onychomys leucogaster*; and western harvest mouse, *Reithrodontomys megalotis*. *Perognathus parvus* composed 84.2% of the total catch, with *P. maniculatus*, *O. leucogaster*, and *R. megalotis* comprising 9.4, 3.4, and 2.9 percent, respectively (Table 1).

The low trapping success in the fall reflects reduced surface activity and the post-breeding mortality of *P. parvus*, the most abundant species. Summer peaks reflect the termination of reproduction in this species and the increased foraging of weaned young. With the exception of *R. megalotis*, species composition was comparable to small mammal populations inhabiting slightly higher elevations on the reservation, where ground cover consists of more native vegetation (O'Farrell et al. 1975). The greater percent of captures of harvest mice on my study area may reflect this species propensity for habitats with a mixture of native and introduced vegetation (Black and Frischknecht 1971). *Peromyscus maniculatus* was the only species taken throughout the year, although it showed considerable seasonal variation in the number of individuals trapped. *Perognathus* *parvus* was conspicuously absent in the coldest winter months (December and January) and *R. megalotis* was not trapped in the fall months of September and October. *Onychomys leucogaster* was captured each month except February, but trapping success for this species and *R. megalotis* never exceeded 1 percent. Other rodent species, including the sagebrush vole, mountain vole, Townsend's ground squirrel, pocket gopher, and bushy-tailed wood rat occur on parts of the reservation but were absent on my study area.

Because of the unpredictability of precipitation and extremes in temperature, desert rodent populations can demonstrate considerable annual fluctuations. The pocket mouse has specifically adapted to this environment (Schreiber 1978a), and the other species, because of their eurytopic habits, are able to survive at low population levels. Even though total population numbers may exhibit large annual oscillations, the proportional distribution of species probably remains stable over the long term.

Energy Budgets and Ingestion Rates

Energy flow 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 thermoneutrality and directly proportional to temperatures above it. Small rodents, with a relatively large body surface to body weight ratio, gain heat from the environment and dissipation of this heat load against a thermal gradient would require evaporative cooling and subsequent water loss, a luxury desert rodents cannot afford. However, these nocturnal animals rarely encounter ambient temperatures that exceed body temperatures (Table 2), so energy expenditure is mainly from thermogenesis and activity. Females experience additional demands during pregnancy and lactation. Seasonal changes in the insulatory

TABLE 1. Monthly trapping results for the Hanford Study Area, Benton County, Washington.

		Species							
		P. parvus		P. maniculatus		O. leucogaster		R. megalotis	
Month	Trap days	No.	Trap success (%)	No.	Trap success (%)	No.	Trap success (%)	No.	Trap success (%)
1969									
Sep.	200	9	(4.5)	1	(<1)	0		0	
Nov.	400	17	(4.2)	1	(<1)	2	(<1)	1	(<1)
1970									
Mar.*	280	50	(17.8)	6	(2.0)	0		1	(<1)
Apr.	297	50	(16.8)	13	(4.4)	2	(<1)	0	
May	298	92	(30.9)	10	(3.3)	3	(1.0)	1	(<1)
June	2216	544	(24.5)	39	(1.7)	19	(<1)	8	(<1)
July	550	166	(33.2)	7	(1.4)	3	(<1)	4	(<1)
Aug.	450	40	(8.9)	8	(1.8)	4	(<1)	1	(<1)
Sep.	1050	48	(4.6)	10	(1.0)	5	(<1)	0	
Oct.	1648	34	(2.1)	8	(<1)	6	(<1)	0	
Nov.	1300	2	(<1)	11	(<1)	1	(<1)	3	(<1)
Dec.	600	0		3	(<1)	1	(<1)	3	(<1)
1971									
Jan.	750	0		7	(<1)	3	(<1)	3	(<1)
Feb.	900	3	(<1)	6	(<1)	0		9	(1.0)
Mar.	750	39	(5.2)	3	(<1)	1	(<1)	4	(<1)
Apr.	950	60	(6.3)	4	(<1)	0		3	(<1)
May	750	47	(6.3)	2	(<1)	0		2	(<1)
Aug.	900	37	(4.1)	0		0		0	
Total	14,289	1,238	(8.7)	139	(1.0)	50	(<1)	43	(<1)

*Heavy rain and strong winds recorded at trapping site properties of the pelage influence metabolic rates, but in small mammals this effect is minimal. Therefore annual energy expenditures of individuals are primarily the result of reproduction.

Reithrodontomys megalotis: This rodent was the smallest of the four species captured and it had a scattered distribution on the study area. Although never abundant, it is an opportunist, which enables it to exploit a variety of microhabitats.

Pearson (1960) calculated resting metabolism (mℓ O_2 g^{-1} hr^{-1}) in this small cricetid as—

$$E_r = 11.41 - 0.27\ T_b\ (T_b < 24.5\ C) \qquad (4)$$

Adding the increment for activity (2.9 ml O_2/g/hr, Chew and Chew, 1970) to E_r,

$$E_a = 14.31 - 0.27\ T_A \qquad (5)$$

Harvest mice construct elaborate, well-insulated nests which reduce energy expended for thermoregulation at lower temperatures. Thus,

$$E_n = 9.2 - 0.18\ T_b\ (T_b < 24.5\ C) \qquad (6)$$

Harvest mice may be gregarious during the colder months; if so, their metabolic costs would be effectively reduced. Without nesting material, huddling can reduce metabolic rates 27–39 percent (Pearson 1960, Trojan and Wojciechkowska 1968). With a nest, huddling reduces energy expended in heat production by about 13 percent (Grodzinski and Gorecki 1967) and significantly lowers food consumption (Gebczynska and Gebczynski 1971). I used the latter figure (13 percent) to determine the savings from huddling in a nest.

Although *R. megalotis* is active throughout the year, its surface activity is presumably reduced during the colder months to minimize thermal stress. A male, with a radioactive tag, was monitored for three nights in November (Table 3). The average time spent above ground was 3.3 hours. I accepted this time as representative of both fall and winter activity. This estimate is probably a maximum because individuals may go several days without any surface activity during inclement weather. In fact, both Pearson (1960) and Gaertner (1968) allude to hypometabolism and possible torpor in *Reithrodontomys*. In the spring and summer, food availability and a more energetically favorable microclimate probably extend surface activity. Activity during these seasons was estimated as 4 hours/night, a value also used by Pearson (1960).

Estimated annual energy expenditure for an individual harvest mouse is shown in Table 4. Daily cost for maintenance in males (mean weight 10.76 g) and females (mean weight 9.48 g) is 9.11 and 8.02 kcal, respectively. This amounts to 0.85 kcal/g/day, of which thermoregulation accounts for about 74 percent and activity for 26 percent. Maintenance costs were 25 percent lower in

TABLE 2. Microenvironmental temperatures at the Hanford Study Area.

			Mean temperature, °C		
			In	At soil surface	
Time interval	Length (days)	Midpoint	burrow (T_b)	Day (T_d)	Night (T_n)
Jun 17–Jun 28	12	Jun 22	24.2	43.9	22.4
Jun 29–Aug 3	36	Jul 16	26.9	40.1	22.5
Aug 4–Sep 10	38	Aug 22	26.0	37.0	18.5
Sep 11–Oct 12	32	Sep 26	19.2	21.6	8.2
Oct 13–Nov 15	34	Oct 29	12.6	8.6	-1.2
Nov 16–Dec 5	20	Nov 25	10.6[a]	-1.8[b]	-5.1[b]
Dec 6–Jan 1	27	Dec 19	8.3[a]	-4.5	-7.3
Jan 2–Feb 4	34	Jan 18	5.6[a]	0.3	-4.5
Feb 5–Mar 12	36	Feb 22	5.6[a]	5.2	-3.6
Mar 13–Apr 11	30	Mar 27	10.0	18.3	2.4
Apr 12–May 11	30	Apr 26	16.5	29.8	11.0
May 12–Jun 16	36	May 29	19.7	32.2	15.7

[a] Temperatures taken at 9 dm (Stone, et al., 1972)

[b] Based on 14 days data

TABLE 3. Activity patterns and average amount of time spent on the surface by a male *Reithrodontomys megalotis.*

Date	Time out	Time in	Elapsed time	Total time[*]
November 27–28	21:26	23:29	2h:03m	2h:03m
	1:30	1:50	0h:20m	0h:20m
	2:43	2:54	0h:11m	0h:11m
	3:54	4:03	0h:09m	0h:09m
	4:45	5:20	0h:35m	0h:35m
	7:08	7:33	0h:25m	0h:18m
			Total	3h:36m
November 28–29	21:16	22:35	1h:19m	1h:01m
	23:40	23:56	0h:16m	0h:16m
	1:50	2:10	0h:20m	0h:20m
	3:37	3:58	0h:21m	0h:21m
	4:42	4:52	0h:10m	0h:10m
	5:47	6:12	0h:25m	0h:23m
			Total	2h:31m
November 29–30	20:10	21:07	0h:57m	Oh:57m
	22:17	22:42	0h:25m	0h:25m
	0:24	0:50	0h:26m	0h:26m
	3:12	4:01	0h:49m	0h:49m
	5:32	6:15	0h:43m	0h:43m
	6:47	7:07	0h:20m	0h:20m
			Total	3h:40m
			Mean time . . .	3h:16m

[*] Elapsed time minus time for periodic retreats to the burrow

TABLE 4. Annual maintenance energy expenditure for *Reithrodontomys megalotis* at the Hanford Study Area. Body weight: males = 10.76 g, females 9.48 g.

Time interval		Hours daily		Metabolic costs (kcal)[a]					
Dates	Days	At rest	Active	Male			Female		
				E_r	E_a	E_m	E_r	E_a	E_m
6/17-6/28	12	20	4	62.0	20.6	82.6	54.6	18.1	72.7
6/29-8/3	36	20	4	159.9	62.5	222.4	140.9	55.0	195.9
8/4-9/10	38	20	4	172.7	73.8	246.5	152.2	65.0	217.2
9/11-10/12	32	20.7	3.3	195.0	66.5	261.5	171.1	58.6	229.7
10/13-11/15	34	20.7	3.3	254.4	84.0	338.4	224.2	74.0	298.2
11/16-12/5	20	20.7	3.3	156.1	52.8	208.9	137.5	46.6	184.1
12/6-1/1	27	20.7	3.3	219.4	74.9	294.3	193.3	66.0	259.3
1/2-2/4	34	20.7	3.3	301.7	89.2	390.9	265.8	78.6	344.4
2/5-3/12	36	20.7	3.3	319.4	92.6	412.0	281.4	81.6	363.0
3/13-4/11	30	20	4	229.3	84.3	313.6	202.0	74.3	276.3
4/12-5/11	30	20	4	195.2	70.6	265.8	172.0	62.2	234.2
5/12-6/16	36	20	4	212.0	75.1	287.1	186.7	66.2	252.9
Annual total (Kcal/yr) without huddling				2477.1	846.9	3324.0	2181.7	746.2	2927.9
(% E_m)				(74.5)	(25.5)		(74.5)	(25.5)	
with huddling				2289.1	846.7	3135.8	2016.2	746.2	2762.4
(% E_m)				(73.0)	(27.0)		(73.0)	(27.0)	

[a] Based on microenvironmental temperatures (Table 2)

the spring and summer than in the fall and winter. For a 9 g individual of this species in central California, Pearson (1960) estimated daily energy costs averaged 7.6 kcal. His lower value reflects both the smaller average weight and the higher microenvironmental temperatures encountered by that population.

The coefficient of digestibility of this species, based on the ash tracer method, was 0.856. After adding the energy cost of preadult growth (E_{g3}), ingestion rate for a male was calculated as:

$$I_m = 3473/0.856 = 4057 \text{ kcal/yr} \qquad (7)$$

Based on a diet of 5.92 kcal/g (mean caloric value of stomach material, Schreiber 1979), a male would consume 686 g per year or about 1.9 g per day.

Weight gains were determined for each growth stage. At birth harvest mice weigh 1.5 g (Svihla 1931). This was increased 0.4 g to account for embryonic tissues. Weaning weight, prorated from that for deer mice, was calculated as 5.4 g. Mean body weight for adult males and nongravid (NG) females was 10.12 g (N = 34). Caloric density for adult tissue was 1.58 kcal/g (Schreiber and Johnson 1975); other caloric values and growth efficiencies were given in the methods. Mean litter size (n) was 3.6 (N = 8), with females producing 1.11 litters per year (L). The annual ingestion rate for a female was calculated as:

$$I_f = (2928 + 318)/0.856 = 3791 \text{ kcal/yr} \quad (8)$$

These mice expend 16.7 percent of this growth energy between conception and birth, 35.7 percent between birth and weaning, and 47.6 percent after weaning. Females would annually consume 642 g or 1.8 g per day based on the above diet. Huddling during the colder months would reduce total energy expenditure 5.7 percent.

Peromyscus maniculatus: Deer mice were the second most abundant rodent in the study area (Table 1). Because this species is also active periodically throughout the year, their activity patterns are presumably similar to those determined for harvest mice. For E_r, I adjusted the minimum rate measured by McNab and Morrison (1963, Table 1 and Fig. 3) by 24.5 percent, as suggested by Chew and Chew (1970), to obtain the average resting metabolism:

$$E_r = 9.3 - 0.2\ T_b\ (T_b > 27.1\ C) \qquad (9)$$

Correcting this for the energy used during activity:

$$E_a = 12.2 - 0.2\ T_A \qquad (10)$$

The insulating effects of a nest reduce E_r to:

$$E_n = 7.4 - 0.13\ T_b\ (T_b < 27.1\ C) \qquad (11)$$

Daily, males require about 14.1 kcal and females 12.1 kcal for maintenance (Table 5) or 0.63 kcal/g/day in the spring and summer.

Adding the growth increment and using a coefficient of digestibility of 0.879 calculated for animals living in the wild, the ingestion rate for males was:

$$I_m = 5344/0.879 = 6080 \text{ kcal/yr} \qquad (12)$$

In addition to maintenance costs, females in the study areas produced an average of 1.32 litters per year with a mean number of 4.7 young (N = 44). At birth, deer mice weigh an average of 1.8 g (Svihla 1934); embryonic tissues add 1.1 g. Weaning takes place in about 25 days, when animals weigh about 11 g (Svihla 1934, Chew and Chew 1970). Mean adult body weight of males and NG females was 17.5 g (N = 162) and adult tissue of this species has a caloric value of 1.56 kcal/g (Schreiber and Johnson 1975). Previously cited values were used for other tissue energy and growth efficiencies. Ingestion rate for females was:

$$I_f = (4425 + 753)/0.879 = 5891 \text{ kcal/yr} \quad (13)$$

Of the 753 kcal used for growth, 16.9 percent was used before birth, 56.1 percent from birth to weaning, and 26.9 percent after weaning. Deer mice on the study area consumed diets with a mean caloric value of 5.75 kcal/ g (Schreiber 1979). Therefore, to meet the required energy demands, males would consume 1.06 kg/yr and females 1.03 kg/yr, or about 2.9 g/day. This amounts to 14.6 percent and 16 percent of the body weight in males and females, respectively. Johnson and Groepper (1970) estimated a 20 g deer mouse in the North Plains consumed 1.9 g of food daily or about 9 percent of its body weight. Deer mice on standard rations at temperatures 10–15 C reportedly consumed an average of 3 g/day (Hatfield, 1940) or 2.8 g/day at 28 C (Sealander 1952).

Energy requirements effecting reproductive stress may substantially increase (e.g., 200 percent) between birth and the end of weaning (Stebbins 1977), so my estimates for females may be somewhat low. Besides huddling, which effectively reduces metabolic costs 5.5 percent (Table 5), deer mice no doubt also resort to additional means of reducing energy expenditure during periods of stress. Marten (1973) found this species may sharply reduce its activity through the summer and activity becomes compressed into the early part of the night, when conditions probably permit a more favorable heat exchange. For the same reason, diurnality may increase in colder months. In winter, pelage (insulation) increases and also contributes to a lower metabolism. Howard (1951) suggested huddling is an important part of energy reduction in deer mice, with torpor occurring in grouped animals. Torpor in this species has also been observed by others (e.g., Morhardt and Hudson 1966, Morhardt 1970). Additionally, Kritzman (1974) and O'Farrell (1975a) suggested possible summer estivation or hypothermia for animals at the Hanford Reservation. Although the rhythmicity of torpor in natural populations is unknown, it could serve both to conserve water in the summer and reduce energy costs at low temperatures or during periods of food scarcity. Hart (1958) also suggested possible alterations in the ability to metabolize food during such periods of stress. As an additional factor, food caches may offer a significant buffer during periods of severe weather and with sufficient stored food, individuals would spend less time on the surface exposed to unfavorable microenvironmental temperatures.

Peromyscus maniculatus is omnivorous, demonstrating marked seasonal variation in its diet (Johnson 1964). On other parts of the reservations this species relied heavily on insects for food from spring until fall (Kritzman 1974), probably switching to a more granivorous diet as this food source diminished. It would appear then that competition for available seeds between this species and the more abundant *P. parvus* would be reduced due to their periods of activity, deer mice becoming more dependent on seeds in the colder months when pocket mice are dormant. Additional research is necessary to properly evaluate these aspects of deer mice energetics.

Onychomys leucogaster: At an average weight of 25 g, the stout-bodied northern grasshopper mouse was the largest rodent species on the study area. It was present in

TABLE 5. Annual maintenance energy expenditure for *Peromyscus maniculatus* at the Hanford Study Area. Body weight: males = 19.17 g, females 16.83 g.

Time interval		Hours daily		Metabolic costs (kcal)[a]					
Dates	Days	At rest	Active	Male			Female		
				E_r	E_a	E_m	E_r	E_a	E_m
6/17-6/28	12	20	4	95.0	34.2	129.2	83.4	30.0	113.4
6/29-8/3	36	20	4	258.4	102.0	360.4	226.8	89.6	316.4
8/4-9/10	38	20	4	283.2	118.9	402.1	248.6	104.4	353.0
9/11-10/12	32	20.7	3.3	301.7	102.5	504.2	264.9	90.0	354.9
10/13-11/15	34	20.7	3.3	378.2	128.5	506.7	332.0	112.8	444.8
11/16-12/5	20	20.7	3.3	232.4	80.3	312.7	204.0	70.5	274.5
12/6-1/1	27	20.7	3.3	329.1	111.9	441.0	289.0	98.2	387.2
1/2-2/4	34	20.7	3.3	433.9	135.2	569.1	380.9	118.7	499.6
2/5-3/12	36	20.7	3.3	459.4	141.0	600.4	403.3	123.8	527.1
3/13-4/11	30	20	4	336.8	130.0	466.8	295.7	114.1	409.8
4/12-5/11	30	20	4	292.6	110.4	403.0	256.9	96.9	353.8
5/12-6/16	36	20	4	324.6	120.6	445.2	285.0	105.8	390.8
Annual total (Kcal/yr) without huddling				3825.3	1315.5	5140.8	3270.5	1154.8	4425.3
(% E_m)				(74.4)	(25.6)		(73.9)	(26.1)	
with huddling				3547.8	1315.5	4863.3	3026.9	1154.8	4181.7
(% E_m)				(73.0)	(27.0)		(72.4)	(27.6)	

[a] Based on microenvironmental temperatures (Table 2)

low numbers throughout the year. Traps holding these mice were often adjacent to those with mutilated pocket mice, indicating *O. leucogaster's* carnivorous tendency and predatory feeding habits. To my knowledge, no metabolic-temperature function equation presently exists for this species, so I used the equation for *O. torridus* (Chew and Chew 1970), a species of similar size. Average resting metabolism is:

$$E_r = 7.24 - 0.17\,T_b\ (T_b > 27.1\ \mathrm{C}) \qquad (14)$$

This species uses a nest (Ruffer 1965) and, assuming Pearson's (1960) correction for its insulating properties,

$$E_n = 5.86 - 2.12\,T_b\ (T_b < 27.1\ \mathrm{C}) \qquad (15)$$

above-ground activity increases energy expenditure; so,

$$E_a = 10.14 - 0.17\,T_A \qquad (16)$$

presumably, this species has periods of activity similar to harvest mice and deer mice. Annual maintenance costs were estimated as 4857 and 5215 kcal for males and females, respectively (Table 6). Generally, metabolic costs are about 25 percent greater in the colder months than in the warmer months. Nest burrows are shared by male-female pairs (Ruffer 1965); such huddling would produce a 5 percent savings in energy.

Males digest an average of 90.3 percent of their caloric diet. E_{g_3} = 303 kcal for this species, so ingestion rate was calculated as:

$$I_m = 5160/0.903 = 5714\ \mathrm{kcal/yr}$$
$$\text{(without huddling)}$$

or

$$= 4893/0.903 = 5419\ \mathrm{kcal/yr}$$
$$\text{(with huddling)} \qquad (17)$$

Grasshopper mice weigh 2.2 g at birth (Svihla 1936), excluding embryonic tissues (~0.6 g). Females raised an average of 1.07 litters per year with a mean litter of 3.3 young (N = 14). Young are weaned at about 23 days at an average weight of 13.2 g (Pinter 1970) and the mean weight of mature males and NG females was 22.6 g. Using a caloric value of 1.61 kcal/g for adult tissue (Schreiber and Johnson 1975) and other values cited earlier, energy cost for growth from conception to subadult is 660 kcal. The majority of this growth energy is expended after birth. Prenatal growth accounted for 10.6 percent, weaning period for 43.5 percent, and postweaning growth for 45.9 percent. With a digestibility coefficient of 0.892, ingestion rate for females is:

$$I_f = (5215 + 660)/0.892 = 6587\ \mathrm{kcal/yr}$$
$$\text{(without huddling)}$$

or

TABLE 6. Annual maintenance energy expenditure for *Onychomys leucogaster* at the Hanford Study Area. Body weight: males = 24.3 g, females 26.2 g.

Time interval		Hours daily		Metabolic costs (Kcal)[a]					
Dates	Days	At rest	Active	Male			Female		
				E_r	E_a	E_m	E_r	E_a	E_m
6/17-6/28	12	20	4	82.6	35.6	118.2	89.0	38.3	127.3
6/29-8/3	36	20	4	219.2	105.0	324.2	236.3	113.2	349.5
8/4-9/10	38	20	4	239.3	124.1	363.4	258.0	133.8	371.2
9/11-10/12	32	20.7	3.3	274.3	107.2	381.5	295.7	115.5	411.2
10/13-11/15	34	20.7	3.3	357.1	134.8	491.9	385.0	145.3	530.3
11/16-12/5	20	20.7	3.3	222.1	83.9	306.0	239.5	90.5	330.0
12/6-1/1	27	20.7	3.3	316.2	117.4	433.6	340.9	126.6	467.5
1/2-2/4	34	20.7	3.3	426.9	142.6	569.5	460.2	153.8	614.0
2/5-3/12	36	20.7	3.3	452.0	147.6	599.6	487.3	159.1	646.4
3/13-4/11	30	20	4	325.4	135.1	460.5	350.9	145.6	495.5
4/12-5/11	30	20	4	272.9	115.5	388.4	294.3	124.5	418.8
5/12-6/16	36	20	4	293.9	126.0	419.9	316.9	135.8	452.7
Annual total (Kcal/yr) without huddling				3481.9	1374.8	4856.7	3733.7	1482.0	5215.4
(% E_m)				(71.7)	(28.3)		(71.6)	(28.4)	
with huddling				3215.6	1374.8	4590.4	3446.3	1482.0	4928.3
(% E_m)				(70.1)	(29.9)		(69.9)	(30.1)	

[a] Based on microenvironmental temperatures (Table 2)

$$(4928 + 660)/0.892 = 6265 \text{ kcal/yr (with huddling)} \tag{18}$$

Males and females which huddle must daily digest 15.6 (0.69) and 17.2 kcal (0.76 kcal/g), respectively. Diets of grasshopper mice include a variety of insects and seeds plus some animal flesh and green vegetation. Stomach material of this species at Hanford had a mean caloric value of 5.22 kcal/g (Schreiber 1979), about 8 percent lower than the value reported for North Plains individuals (Johnson and Groepper 1970). Based on this caloric diet each male and female in the population studied would annually consume about 1038 g (2.9) and 1200 g (3.3 g/day) of food, respectively. By comparison, in the laboratory on diets of beef liver (72 percent water), grasshopper mice consumed 4.1 g/day (Whitford and Conley 1971).

The incidence of seeds in the diet of this species may significantly increase in the fall and winter (Flake 1971), suggesting it relies on seed caches when insects are less available. Less surface activity would decrease metabolic demands in the colder months. To facilitate this energy savings individuals may restrict more of their winter "hunting" activity to burrow systems. Burrows serve as hibernacula for insects, lizards, and torpid mice, all potential food sources for *O. leucogaster*. The generally high fat deposits of this rodent probably conserve body heat when it is forced to be active on the surface during the cold months.

Ecological Relationships

Individually, *P. maniculatus* and *O. leucogaster* process between 2½ to 3 times as much energy during the year as *P. parvus*, the most common species (Table 7). The smaller size of the pocket mouse and its periodic use of torpor account for this difference. Based on the relative numbers of individuals (Table 1), however, *P. parvus* dominates as the primary "energy mover" in the small mammal community of this cold desert ecosystem. At the population level, the annual contribution of pocket mice to community energy exchange is nearly 4 times that of deer mice, 11 times that of grasshopper mice, and about 17 times that of harvest mice. Even at high population levels, however, the granivorous pocket mouse does not significantly affect its primary food resource, cheatgrass (Schreiber 1978b). Thus, it is reasonable to assume the euryphagic and less abundant species represented in this paper would also have an insignificant impact on their diverse food resources.

These results additionally refine our understanding of energetics of small mammal com-

TABLE 7. Estimated annual ingestion rates of selected Great Basin rodents.

Species	Sex	E_m[a] (kcal/yr)	Coefficient of digestibility	Mean litter size	Number litters per year	Energy for growth (kcal)	Ingestion rate	
							(kcal/yr)	(kg/yr)[b]
Perognathus[c] parvus	M	2010	0.892			205	2483	0.50
	F	1774	0.911	3.9	1.10	360	2342	0.47
Peromyscus maniculatus	M	5141	0.879			203	6080	1.06
	F	4425	0.879	4.7	1.32	753	5891	1.02
Onychomys leucogaster	M	4857	0.903			303	5714	1.09
	F	5215	0.892	3.3	1.07	660	6587	1.26
Reithrodontomys megalotis	M	3324	0.856			148	4057	0.68
	F	2928	0.856	3.6	1.11	318	3791	0.64

[a] Maintenance energy (E_m) is calculated without the advantage of savings from hudding.
[b] Based on the mean caloric values of diets of wild mice (Schreiber, 1979)
[c] Taken from Schreiber (1978b)

munities. Unfortunately, the question of the ecological significance of these consumers remains unanswered and a matter of considerable discussion (e.g., Naumov 1975, Chew 1978). As deserts come under increasing pressure for development, the understanding of community function and of the relative cost/benefit of perturbing its various components becomes imperative. Research must now focus on integrating information on bioenergetics with other parameters, such as resource allocation, nutrient cycling and inter- and intraspecific competition, and developing new hypotheses on the role of small mammal consumers.

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