

R. Kent SCHREIBER & Donald R. JOHNSON

**Seasonal Changes in Body Composition and Caloric Content
of Great Basin Rodents ***

[With 5 Tables & 1 Fig.]

Body composition and caloric content were examined in six species of rodents common in the northern Great Basin desert: *Perognathus parvus*, *Eutamias minimus*, *Peromyscus maniculatus*, *Reithrodontomys megalotis*, *Onychomys leucogaster* and *Dipodomys ordi*. A total of 920 individuals were analyzed for seasonal variation in ash content, fat, water, lean dry tissue and live weight caloric content. Although seasonally active and year-round active species exhibit somewhat different trends in body composition, the differences were not usually significant. Ash content ranged from 3.0 to 4.6 per cent of the total body weight, demonstrating no significant differences between species or seasons. Mean water content averaged from 58.7 to 71.9 per cent of the body weight. Seasonally active species (*P. parvus*, *E. minimus*) demonstrated significant declines in the percentage of body water prior to winter torpor. Rehydration in the spring was apparently associated with ingestion of green vegetation. Fat content varied widely, ranging from 1.1 to 13.1 per cent of the total weight. Values were generally lower than those reported for species from more mesic habitats. Fall fat deposition in *P. parvus* and *E. minimus* was insufficient to serve as a winter energy reserve but may be critical as insulation during torpor. Lean dry tissue comprised 23.8 to 27.6 per cent of the body weight, demonstrating little seasonal variation. Its energy content ranged from 4.50 to 4.89 kcal/g. Linear regression equations describing the relationship of body components to body weight are given. Generally, live weight caloric content (kcal/g body weight) varied directly with fatness and inversely with body hydration. Annual mean values for adults were 1.55 kcal/g in *P. parvus*, 1.61 in *O. leucogaster*, 1.56 in *P. maniculatus* and 1.58 in *R. megalotis*. Values for *E. minimus* and *O. ordi* taken in the summer and fall averaged 1.49 and 1.39 kcal/g, respectively.

I. INTRODUCTION

Rodents are an important component in the consumer populations of arid regions. They form an important link in the desert food chain and

* This work is a part of the U.S.-International Biological Program, Desert Biome and is Contribution No. 190 from the Eastern Deciduous Forest Biome. Publication No. 670, Environmental Sciences Division, Oak Ridge National Laboratory.

serve as functional regulators in the transfer of some energy through the ecosystem. This transfer is not only a function of the rate of energy expenditure for maintenance and activity, but is also a function of the accumulation of energy (kcal/g live body weight) and its rate of turnover. Determination of seasonal variation in body composition and caloric content is therefore a prerequisite to comprehensive investigations of energy transfer in desert rodents. Several recent studies have dealt with the bioenergetics of rodents in arid regions (e.g., Chew & Chew, 1970; Kenagy, 1973; and Soholt, 1973) but little data exist on body composition and seasonal fat deposition in such species.

Objectives of this study were: 1) to determine gross body composition; 2) to describe seasonal fat cycles, 3) to determine live weight caloric content, and 4) to derive equations describing the seasonal relationships between body weight and gross body components (i.e., water content, lean dry content, fat) of six species of northern Great Basin desert rodents [i.e., deer mouse (*Peromyscus maniculatus*), Great Basin pocket mouse (*Perognathus parvus*), harvest mouse (*Reithrodontomys megalotis*), northern grasshopper mouse (*Onychomys leucogaster*), least chipmunk (*Eutamias minimus*) and Ord kangaroo rat (*Dipodomys ordii*)].

II. MATERIALS AND METHODS

Rodents were collected from September 1969 to August 1971 at the Hanford Atomic Energy Commission reservation (Benton County) near Richland, Washington and from May to November 1971 in the Curlew Valley of southern Idaho (Oneida County) and northern Utah (Box Elder County). These areas are characterized by low annual rainfall (15–25 cm) with hot, dry summers and cold winters. Predominant woody vegetation includes big sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*) and rabbitbrush (*Chrysothamnus nauseosus* and *C. viscidiflorus*). Common grasses are cheatgrass (*Bromus tectorum*) at Hanford and crested wheatgrass (*Agropyron cristatum*) and Idaho fescue (*Festuca idahoensis*) at Curlew Valley.

Animals were collected using Museum Special traps baited with rolled oats paste. Sex, weight and reproductive status were recorded for each animal. Age classes (adult and immature) were established by weight and pelage. All gravid or lactating females were considered adults and were treated separately. Specimens were frozen in plastic bags prior to laboratory analysis.

Carcasses were split midventrally, stomach contents removed and initial body weight recorded. Specimens were dehydrated in a vacuum oven to a constant weight at 70°C. The dried carcass was crushed and sewn between two pieces of filter paper for fat extraction in a Soxhlet apparatus using anhydrous diethyl ether as the solvent. Following extraction, packets were dried to a constant weight and the fat content calculated by subtraction. The remaining lean dry residue was ground in a Wiley mill (40 mesh/inch screen) and ash content determined by combustion in a muffle furnace at 600°C for 2 hours. Caloric values of the lean dry tissues were ascertained by combustion in a Parr semi-micro oxygen bomb calorimeter charged to 35 atmospheres. Samples were dried for approximately 24 hours at 50–60°C, pressed

into pellets and the average of 3 firings used as the caloric equivalent of the tissue. Live weight caloric content of the carcass was calculated as the sum of the caloric values of the fat and lean dry body weight fractions divided by the total weight of the animal. A caloric value of 9.2 kcal/g was accepted for fat tissue (Sawicka-Kapusta, 1968).

Body composition and caloric content of rodents have been expressed variously as percent of the dry weight (Górecki, 1965; Sawicka-Kapusta, 1968; Myrcha, 1968; Fleharty, *et al.* 1973), fat-free body weight (Babineau & Page, 1955; Bailey, *et al.*, 1960; Pitts, 1960, 1962; Hayward, 1965 and Blake, 1972), lean dry («basic») body weight (Jameson & Mead, 1964; Myrcha, 1969; Ewings, *et al.* 1970 and Evans, 1973), carcass weight (excluding head, skin and gut content) (Pitts & Bullard, 1968; Pucek, 1973) and wet (fresh) or total body weight (Forbes, 1966; Myrcha, 1969; Startin, 1969; Morton & Tung, 1971; Yousef & Dill, 1970, 1971 and Scott, *et al.* 1972). The latter method of comparison was used since it provided a straightforward ratio and permitted direct calculation of regression equations for predicting body composition from live weight.

The Duncan new multiple range test was used to test for statistical significance in comparisons of intra- and inter-specific values and seasonal differences in body composition. Significance is indicated at the 5% level.

To determine the relationship and predictability of body components (Y) based on fresh or live body weight (X), data were analyzed by linear and curvilinear regression. Preliminary treatment showed no significant improvement in fit by curvilinear regression so simple linear regression ($Y=a+bX$) was used. *P. parvus*, *P. maniculatus* and *E. minimus* were analyzed by month or meteorological season, *i.e.*, spring (March—May), summer (June—August), fall (September—November) and winter (December—February). Because of small sample size for *R. megalotis*, *O. leucogaster* and *D. ordii*, data for each species were pooled for the entire year and single regression equations derived for each sex. Regression equations are presented in the appendix.

For analysis, species were separated on the basis of annual activity patterns, that is whether they normally exhibited torpor. This distinction is somewhat arbitrary but points out some of the physiological differences exhibited by the rodents. Although some evidence indicates both *Reithrodontomys spp.* (Pearson, 1960; Gaertner, 1968) and *P. maniculatus* (Morhardt & Hudson, 1966; Hudson, 1967; Morhardt, 1970) exhibit at least short periods of torpor, we have treated them together with *D. ordii* and *O. leucogaster* as non-dormant species since they are active during all months of the year. *P. parvus* and *E. minimus* demonstrate facultative torpor, *i.e.*, they remain active as long as it is energetically feasible. *E. minimus* is active late into the fall, exhibiting periodic arousal and above-ground activity during the winter and only sporadic torpor the rest of the year. On the other hand, consistent winter and daily torpor is well documented in *P. parvus* (Iverson, 1967; Guthrie, 1972).

III. DISCUSSION OF RESULTS

A carcass is composed of four major components: (1) ash, (2) water, (3) ash-free lean dry tissue, and (4) fat. Only the latter two furnish energy but changes in the water content or ash indirectly affect caloric

content. Values for live weight caloric content represent the amount of energy available to the next trophic level and respond to the combinatorial effect of fat deposition, body hydration and lean dry tissue. As fat contains nearly twice the calories of lean dry tissue, changes in fat content will have a proportionally greater influence on caloric status.

Mineral composition (ash) of all six species ranged from 3.0—4.6% of the total body weight and showed no significant differences between species or seasons. Values were similar to those reported for other species (e.g., Bailey *et al.* 1960; Górecki, 1965; Fleharty *et al.* 1973) and support the suggestion that this component varies within narrow limits in small mammals. It is reasonable, therefore, to assume ash content has no appreciable effect on seasonal variation in live weight caloric content.

1. Species Seasonally Active

Water

P. parvus and *E. minimus* had their greatest water content in July, when temperatures were highest at the study sites, apparently reflecting the degree of water conservation afforded by reduced surface activity and estivation. Conversely, both species showed dehydration in the fall (Fig. 1). This loss of body water may be important in reducing cellular metabolism during torpor and in increasing over-winter survival by lowering the body's freezing point.

The water content of *E. minimus* in September, October and November was significantly lower than values in July, a decrease from 71.2 to 64.4% in the 5-month span. Similar results have been reported in other sciurids. The water loss may be partly associated with the 5—9% increase in fall weight. Willem's (1971) reported an increase in body size in *E. minimus* significantly increased the rate of water loss per unit body weight. Although no sample was available for the spring and early summer, data for other *Eutamias* indicates spring rehydration (Jameson & Mead, 1964) with recurrence of above-ground activity.

Torpor in *P. parvus* begins in September and lasts until February and March. Animals trapped in these colder months showed significantly lower water content than animals trapped in other seasons (Fig. 1). The mean water content of animals emerging in March was significantly greater than animals in the fall months, indicating rehydration following ingestion of green vegetation. Startin (1969) found a clear correlation between increased consumption of green vegetation and increased body water in *Dipodomys merriami*. On the average, gravid or lactating females exhibited greater water content than non-gravid females, something one might expect due to the amniotic fluid and higher water content of embryos.

Fat

Both torpor-exhibiting species showed a propensity for fat accumulation in the fall (Fig. 2). However, total body fat accounted for a relatively small percent of the total body weight, ranging from about 1.3—9.1% in *P. parvus* and from about 1.1—5.4% in *E. minimus*. These fat deposits would be insufficient to serve as a major energy reserve during cold weather even with extensive periods of torpor (Schreiber, 1973). Nonetheless, fat may effectively increase insulation and may be of primary importance following spring emergence when food is scarce.

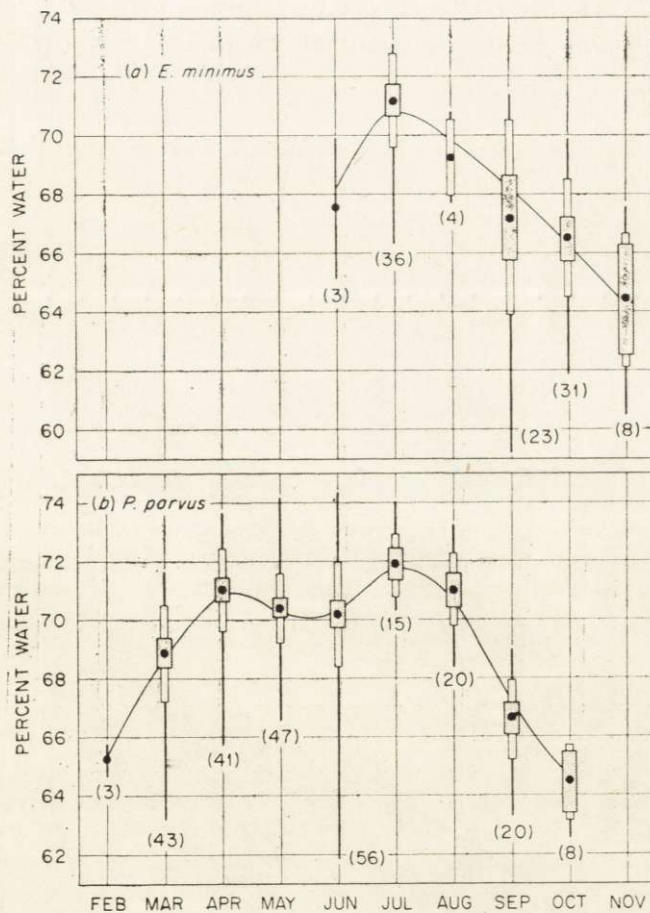


Fig. 1. Monthly variation in water content expressed as percent of the total body weight in adults of two species of seasonally active desert rodents. The solid dot represents the mean; wide bar, the 95% confidence limits; narrow bar, one standard deviation from the mean; vertical line spans the range of values. Numbers in parentheses indicate sample size. Trend lines are hand drawn.

Winter survival is possible because of intermittent torpor and reliance on extensive food caches.

In *E. minimus* fat deposition increased rapidly between September and November, a 41% increase in total body fat in 3 months (Fig. 2). Forbes (1966) reported a 100% increase in body fat from July to October in this species in Minnesota. Corresponding autumnal increases have been recorded in other chipmunks (Tevis, 1966; Panuska,

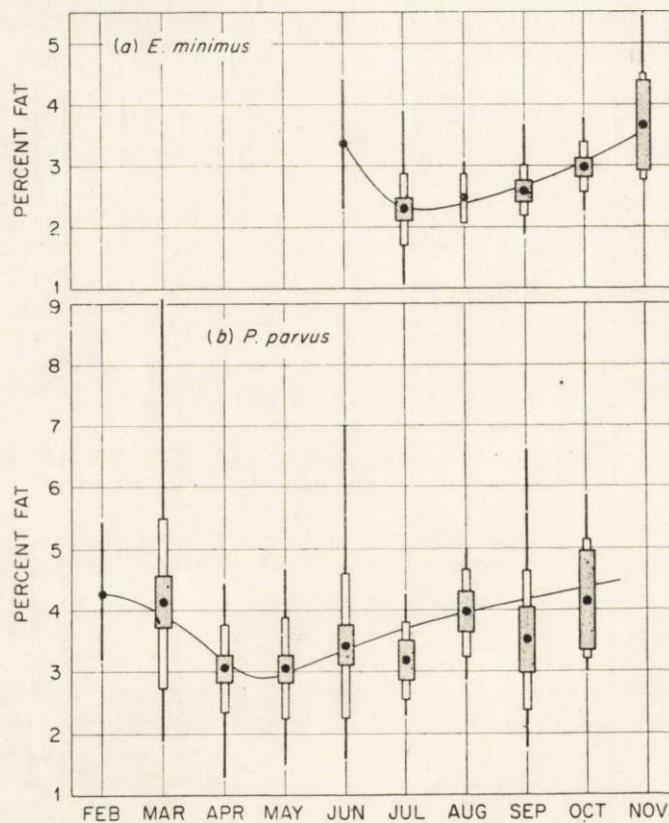


Fig. 2. Monthly variation in fat content expressed as percent of the total body weight in adults of two species of desert rodents active seasonally. Other symbols as in Fig. 1.

1959; Cade, 1963; Jameson & Mead, 1964). Fat content in July was significantly lower than in October and November. Values for October and November were significantly different and indicate the accelerated fall storage. Behavioral and physiological adjustments such as reduction of activity and respiration in response to low temperatures

no doubt facilitate this fat deposition as would cessation of reproduction. Being diurnal, any fall activity probably occurs during the highest daily ambient temperature when energy expenditure is minimized (*i.e.*, nearest thermoneutrality). This species also consumes a high caloric diet in the fall months (Schreiber, 1973).

The fat content of *P. parvus* varied little during the 10 months animals were active above ground, although seasonal trends were evident (Fig. 2). Highest fat levels occurred before and after winter dormancy. Values were the lowest during the peak of reproductive activity in April and May. Gravid or lactating females showed generally higher monthly mean

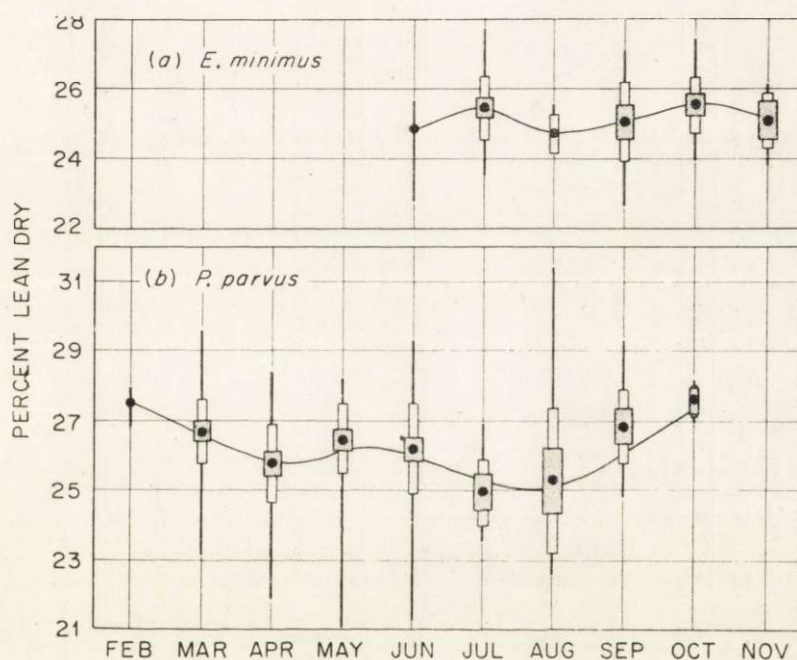


Fig. 3. Monthly variation in lean dry content expressed as percent of the total body weight in adults of two species of seasonally active desert rodents. Other symbols as in Fig. 1.

fat content than non-reproductive females and males but differences were not significant. Likewise, values for immature animals were not statistically different from adults.

Lean Dry Component

This body constituent represents the metabolically active tissue of the animal. Monthly variations in *E. minimus* amounted to less than 1% change and were not significantly different (Fig. 3). These results compare

favorably with those for other species of *Eutamias* (Jameson & Mead, 1964). Caloric value (\pm SE) of this tissue averaged $4.89 (\pm 0.02)$ kcal/g.

In *P. parvus* monthly differences were more evident, the highest values occurring in the late fall and early spring (and presumably over the winter) and lowest values occurring in the summer (Fig. 3), similar to trends reported in kangaroo rats (Startin, 1969; Yousef & Dill, 1971). Percentages for July and August were significantly different from fall months. Likewise, the April value differed statistically from

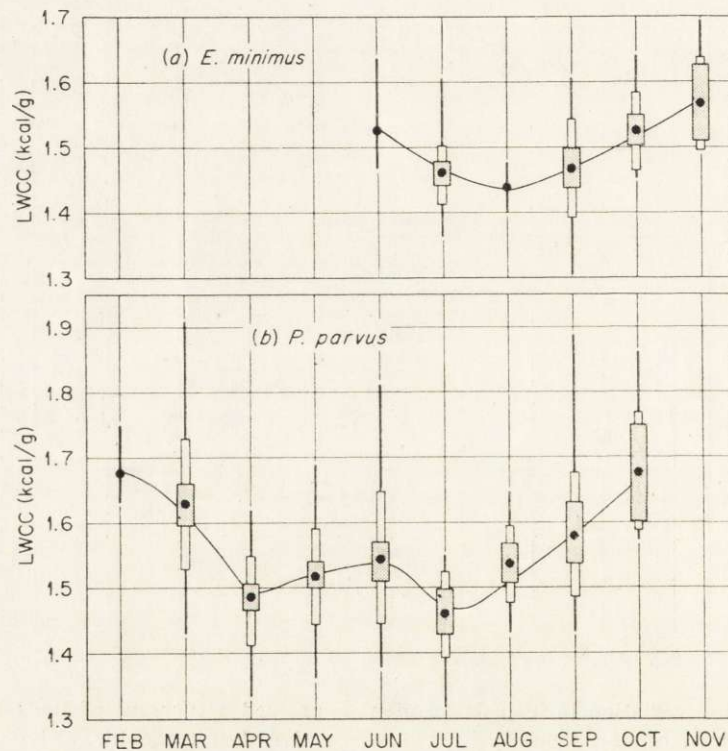


Fig. 4. Monthly variation in live weight caloric content (LWCC) expressed in kilocalories per gram of body weight in adults of two species of seasonally active desert rodents. Other symbols as in Fig. 1.

March and May, possibly denoting a period of physiological transition from winter dormancy to above-ground foraging and incipient reproductive activity. Part of the seasonal change in lean dry composition (protein) may also be associated with seasonal molts. Caloric content of this tissue averaged $4.68 (\pm 0.05)$ kcal/g.

Live Weight Caloric Content

Energy content of *E. minimus* and *P. parvus* reflect the degree of fatness and body hydration. Mean caloric content (kcal/g total body weight) in *E. minimus* showed a 7% increase from July to November (Fig. 4), corresponding to increased fat levels and body dehydration from summer to fall (Fig. 1, 2). The November mean caloric value was significantly higher than those for July, August and September. In a similar manner, *P. parvus* exhibited an increase in live weight caloric content from summer to fall and evidently retained these higher values until the early spring (Fig. 4). On a kcal/g basis, values for the colder months (October, February, March) are significantly higher than those for other months when the species is active above ground. The values for February and October exceed July values by 13%. In general, peaks in energy content were directly related to fat levels and inversely related to water content.

The annual mean live weight caloric contents for adult, gravid/lactating and immature animals are summarized in Table 1. In *P. parvus*, values were highest in adults and lowest in immatures; however, differences between age classes were not significant. Likewise, values for *E. minimus* demonstrated no significant differences.

2. Species Active Year-around

Water

In the four species of rodents active all year, body water ranged from 53.5 to 73.8% of the total body weight, demonstrating seasonal and interspecific differences (Fig. 5). *P. maniculatus* showed a gradual increase in the percent of body water from spring to fall. The fall peak was significantly different from the spring and summer means. In *R. megalotis*, the peak occurred in the summer. Body water then declined steadily to the winter low, a trend also reported in populations in the Great Plains (Flehart, et al. 1973). The significant decline in body water from the summer to winter indicates this species undergoes substantial dehydration in the colder months. If dehydration is one of the prerequisites for torpor, such a trend supports suggestions (Pearson, 1960; Gaertner, 1968) that cold weather torpor occurs in *Reithrodontomys*. Interestingly, populations of *R. megalotis* and *P. maniculatus* from the Great Plains showed consistently higher water content than those from the Great Basin, suggesting that body hydration is related to the aridity of the habitat. Hayward's data (1965) for six geographic races of *Peromyscus* also imply this correlation. Additional comparative

Table 1
Annual mean live weight caloric content ($\pm SE$) of six species of rodents from the northern Great Basin. Parentheses enclose the 95% confidence limits.

<i>P. parvus</i>	Species seasonally active			Species active year-round		
	<i>E. minimus</i> ¹	<i>O. leucogaster</i>	<i>P. maniculatus</i>	<i>R. megalotis</i>	<i>D. ordii</i> ¹	
1.547 \pm 0.014 (1.560 - 1.530) N=253	1.489 \pm 0.007 (1.502 - 1.475) N=105	1.614 \pm 0.30 (1.676 - 1.551) N=38	Adult ² 1.556 \pm 0.012 (1.581 - 1.531) N=148	1.583 \pm 0.019 (1.623 - 1.543) N=34	1.390 \pm 0.011 (1.413 - 1.368) N=19	
1.517 \pm 0.10 (1.536 - 1.497) N=97	1.531 \pm 0.039 (1.654 - 1.408) N=4	Gravid or lactating 1.448 \pm 0.043 (1.542 - 1.354) N=14	1.476 \pm 0.016 (1.507 - 1.445) N=73	1.497 \pm 0.043 (1.596 - 1.397) N=9	1.361 \pm 0.041 (1.451 - 1.271) N=12	
1.503 \pm 0.014 (1.530 - 1.476) N=80	1.410 \pm 0.033 (1.552 - 1.268) N=3	Immature ² 1.494 \pm 0.026 (1.548 - 1.439) N=24	1.425 \pm 0.058 (1.674 - 1.175) N=3	1.327 \pm 0.071 (1.553 - 1.101) N=4		

¹ Values based on partial year's data; ² Male and females combined in sample.

studies of inter- and intraspecific geographic differences in body composition of rodents are needed to test this hypothesis.

Dehydration was consistent from spring to winter in *O. leucogaster*; means for spring and summer were significantly higher than those of the fall and winter. Water content was significantly higher in the spring and summer and significantly lower in the fall and winter than that of *P. maniculatus*. The low winter values of *O. leucogaster* and *R. megalotis* were significantly different. Winter dehydration in the latter two

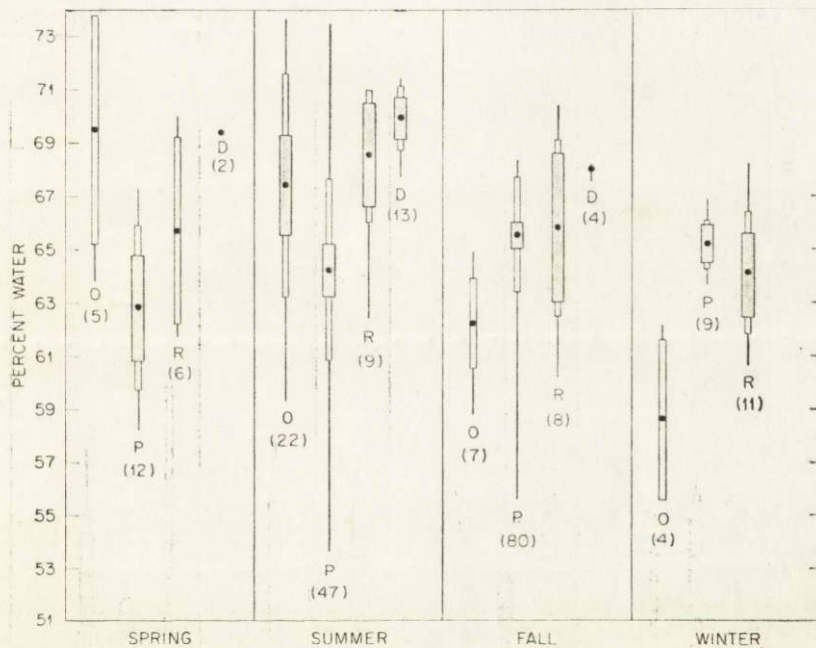


Fig 5. Seasonal variation in water content expressed as percent of the total body weight in adults of four species of desert rodents active year-around. O = *Onychomys leucogaster*, P = *Peromyscus maniculatus*, R = *Reithrodontomys megalotis* and D = *Dipodomys ordii*. Other symbols as in Fig. 1.

species may result, in part, from the switch in diet from insects with high water content to consumption of seeds which contain less water and require more water for metabolism.

Limited data for *D. ordii* suggested a cycle similar to that of *D. merriani* where animals showed lower water content in the colder months than in the warmer months (Startin, 1969; Yousef & Dill, 1970, 1971). Compared to the other non-hibernating species of rodents, this species averaged higher percentages of body water (Fig. 5). This,

no doubt, reflects its known behavioral and physiological adaptations for conserving water.

Fat

Fat content was highly variable in the four species; individual values ranged from 1.3 to 13.1% of the total body weight (Fig. 6). *P. maniculatus* showed a discernible decrease in the percentage of body fat from spring to winter; the two extreme values were significantly different. *R. megalotis* averaged higher fat content than *P. maniculatus* except in the spring whereas, in Kansas, Fleharty, *et al.* (1973) reported consistently higher values in *P. maniculatus*. Mean values for both species were

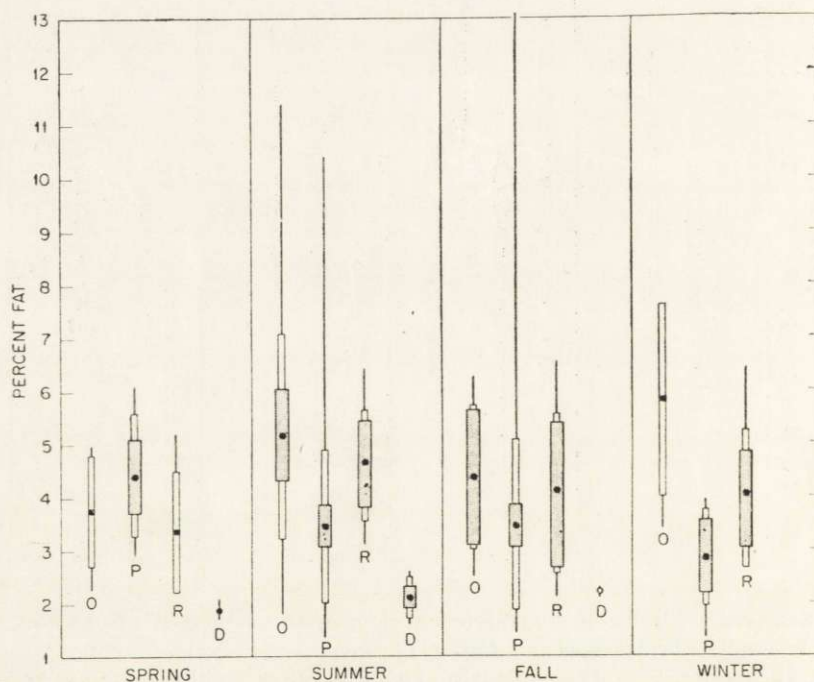


Fig. 6. Seasonal variation in fat content expressed as percent of the total body weight in adults of four species of desert rodents active year-around. Other symbols as in Fig. 1.

lower than those reported for Kansas grassland populations. Mean values for *O. leucogaster* were significantly greater than those for *P. maniculatus* in the summer and winter and were uniformly higher than mean seasonal values for *R. megalotis* and *D. ordii*. *D. ordii* showed little change in fat content. Its fat values were significantly lower than the other three species and were also lower than those values reported in other

species of kangaroo rats (Startin, 1969; Yousef & Dill, 1970, 1971; Scott, *et al.* 1972; Breyen, *et al.* 1973; Soholt, 1973).

In general, all six species in this study averaged lower fat levels than species from more mesic habitats (*e.g.*, Connell, 1959; Hayward, 1965; Gaertner, 1968; Fleharty, *et al.* 1973). Although we lack sufficient long-term data to speculate on the possible evolutionary significance of these apparent low fat levels, others (Hsia-Wu-ping & Sun-Chung-lu, 1963; Fleharty, *et al.* 1973) have suggested lipid cycles may denote physiological adaptation to regional environmental conditions which in turn influence geographic range of the species. Before

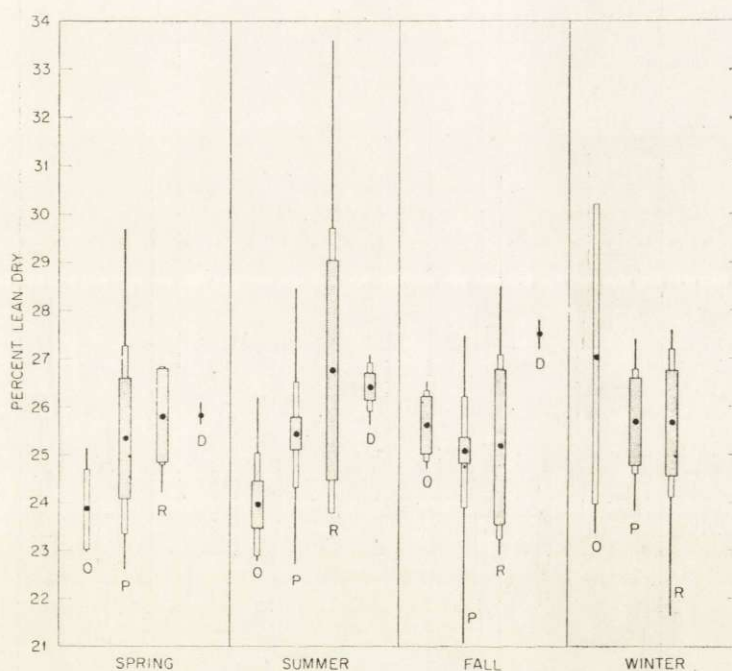


Fig. 7. Seasonal variation in lean dry content expressed as percent of the total body weight in adults of four species of desert rodents active year-around. Other symbols as in Fig. 1.

this question can be resolved, species must be collected over a sufficient span of time to demonstrate any effective seasonal or yearly changes in body composition in concert with related trends in food (energy) availability. For example, Pucek (1973) has recently shown that fat levels varied seasonally in two species of forest rodents but that these seasonal cycles differed significantly from year to year.

Lean Dry Component

Species active above ground the entire year showed only slight seasonal variation in the lean dry component (Fig. 7). Means for spring/summer and fall/winter in *O. leucogaster* were significantly different, reflecting the effects of cold weather dehydration. Average values for *R. megalotis* and *P. maniculatus* were similar and remained mostly stable throughout the year. A trend for a relative increase in lean dry composition from spring to fall was evident in *D. ordii*, corresponding to that reported in *D. merriami* (Startin, 1969; Yousef & Dill, 1971).

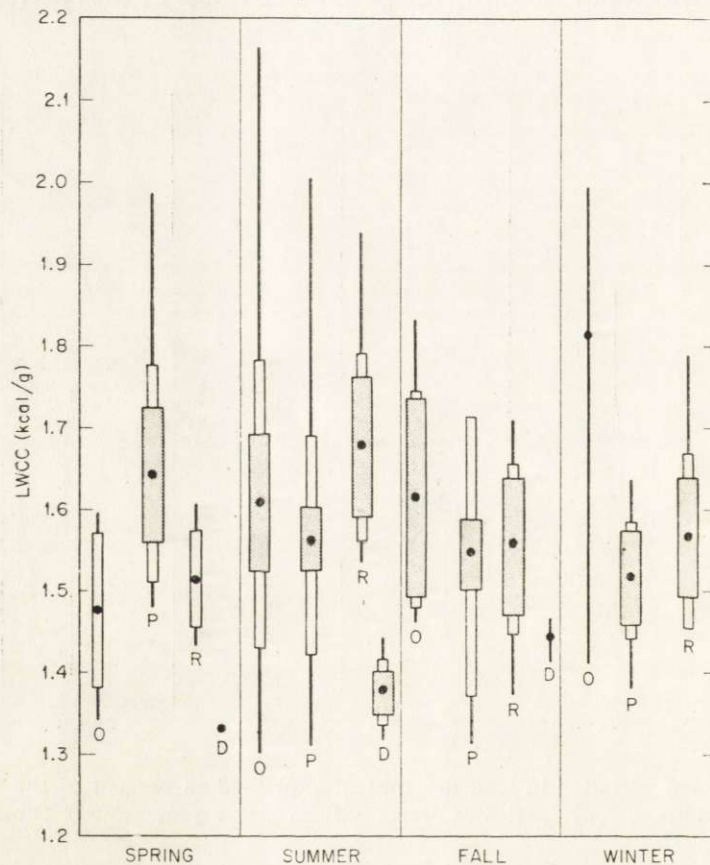


Fig. 8. Seasonal variation in live weight caloric content (LWCC) expressed in kilocalories per gram of body weight in adults of four species of desert rodents active year-around. Other symbols as in Fig. 1.

In the desert where precipitation is scant and erratic, food may be a factor limiting fat content (Schreiber, 1973). Hence, leanness may be a natural condition in desert rodents and may contribute to their observed ability to forage efficiently and avoid predation.

Tissue caloric equivalents in kcal/g (\pm SE) were: 4.73 (\pm 0.10) *O. leucogaster*, 4.89 (\pm 0.13) *P. maniculatus*, 4.66 (\pm 0.07) *R. megalotis* and 4.50 (\pm 0.05) *D. ordii*.

Live Weight Caloric Content

Energy content of these four species (Fig. 8) showed close agreement with values reported for other rodents (Flehart, *et al.* 1973 and the literature cited there). Values for *P. maniculatus* decreased 8% from spring to winter, paralleling fat trends; however, seasonal differences were not significant at the 5% level. *O. leucogaster* showed an opposite trend, caloric content increasing by 23% from spring to winter; the extreme values were significantly different. The summer mean for *R. megalotis* was significantly higher than that of the other three seasons, an annual pattern which is the converse of that shown in grassland populations (Flehart *et al.* 1973). Caloric values for *D. ordii* were the lowest of all species in the study, the combined result of generally high body hydration and exceedingly low fat content. Although its values were consistently lower than those given for *D. merriami* from the Mojave desert (Soholt, 1973), there was apparently a similar trend toward greater caloric content in the colder months.

Annual mean live weight caloric equivalents are given in Table 1. In general, values were highest for adults followed by gravid/lactating females and immatures. Because of its relatively small amounts of body fat adult *D. ordii* showed significantly lower caloric values than adults of the other five species.

3. Comparisons

Comparison of data indicates that although seasonally active and year-around active species exhibit somewhat different trends in body composition, the differences are not usually significant. Of the six species investigated, *P. maniculatus* showed the least amount of annual variation in body composition. This low profile of change may be related to its opportunistic feeding, that is, its relative ease in switching diet as the seasons change and thereby taking advantage of the available sources of energy (*e.g.*, insects, seeds, foliage, fungus). *P. parvus* and *E. minimus*, which undergo winter torpor and summer estivation, demonstrated the most discernible fluctuations in body composition.

Body water decreased in the winter in all species except *P. maniculatus* which showed only a slight decline from the fall. The inverse relationship between body water and fat, as demonstrated in some rodent species (Sealand, 1951; Hayward, 1965; Buckner & Bergeron, 1972), was obvious in *P. parvus* and *E. minimus* but was not apparent in the species active year-around. Seasonal changes in fat content were

evident in all species but the amplitude of change and the amount of fat deposited were insignificant in terms of an energy reserve for use during inclement weather or food scarcity. Fat deposition prior to winter torpor in *P. parvus* and *E. minimus* may provide the insulatory advantage necessary to ensure overwinter survival of viable populations. Similar winter accumulation of fat in *O. leucogaster*, a species active all year, may reflect reduced above-ground activity, lower metabolism and hunting activity more restricted to burrow systems which serve as hibernacula for insects, lizards and torpid mice — all potential food resources. All species demonstrated relatively low fat levels, indicating little energy in excess of that required for maintenance, growth and reproduction is available for storage. All species except *E. minimus* showed at least a small increase in lean dry composition during the fall. Some variation of this body component through the seasons may be the result of growth and chemical maturation of the young adults entering the population.

Annual mean live weight caloric contents of adult *P. parvus*, *O. leucogaster*, *R. megalotis* and *P. maniculatus* showed no significant differences (Table 1). Values were in close agreement with those reported in other rodent species (Górecki, 1965; Fleharty, *et al.* 1973). *O. leucogaster* had the highest live weight caloric values, apparently the result of its generally higher percent of body fat. In shrews caloric content of the body is dependent on body hydration and independent of body fat content (Myrcha, 1969). Our data, however, indicates caloric content in Great Basin rodents responds to both body hydration and fat accumulation. Therefore accurate calculation of seasonal net productivity in these species necessitates the use of seasonal live weight caloric content incorporating changes in both body hydration and fat composition.

Acknowledgments: This work was supported in part through the US/IBP Desert Biome program, under Grant # GB 15886 from the National Science Foundation. Analysis of data was conducted while the senior author was a NORCUS Laboratory Thesis Participant [U. S. Atomic Energy Commission, Contract No. AT(45-1)-2042] with Battelle, Pacific Northwest Laboratories, Ecosystem Department. Final preparations were supported by the Eastern Deciduous Forest Biome, US-IBP, funded by the National Science Foundation under Interagency Agreement AG-199, 40-193-69 with the Atomic Energy Commission — Oak Ridge National Laboratory (operated by Union Carbide Corporation for the U.S. Atomic Energy Commission). We thank Drs. J. W. Huckabee and R. I. Van Hook for critically reviewing the manuscript.

REFERENCES

1. Babineau L. M. & Page E., 1955: On body fat and water in rats. *Canad. J. Biochem. Physiol.*, 33: 970—979.
2. Bailey C. B., Kitts W. D. & Wood A. J., 1960: Changes in the gross chemical composition of the mouse during growth in relation to the assessment of physiological age. *Canad. J. Anim. Sci.*, 40: 143—155.
3. Blake B. H., 1972: The annual cycle and fat storage in two populations of golden-mantled ground squirrels. *J. Mammal.*, 53: 157—167.

4. Breyen L. J., Bradley W. G. & Yousef M. K., 1973: Physiological and ecological studies on the chisel-toothed kangaroo rat, *Dipodomys microps*. *Comp. Biochem. Physiol.*, 44A: 543—555.
5. Buckner C. H. & Bergeron J. M., 1972: Body water and fat content in the redback vole. *Acta theriol.*, 17, 20: 267—269.
6. Cade T. J., 1963: Observations on torpidity in captive chipmunks of the genus *Eutamias*. *Ecology*, 44: 255—261.
7. Chew R. M. & Chew A. E., 1970: Energy relationships of the mammals of a desert shrub (*Larrea tridentata*) community. *Ecol. Monogr.*, 40: 1—21.
8. Connell C. E., 1959: Seasonal lipid levels in three population groups of old-field ecosystem. Ph. D. dissertation, Univ. of Georgia, Athens. 107 p.
9. Evans D. M., 1973: Seasonal variations in the body composition and nutrition of the vole, *Microtus agrestis*. *J. Animal Ecology*, 42: 1—18.
10. Ewings W. G., Studier E. H. & O'Farrell M. J., 1970: Autumn fat deposition and gross body composition in three species of *Myotis*. *Comp. Biochem. Physiol.*, 36: 119—129.
11. Fleharty E. D., Krause M. E. & Stinnett D. P., 1973: Body composition energy content, and lipid cycles of four species of rodents. *J. Mammal.*, 54: 426—438.
12. Forbes R. B., 1966: Fall accumulation of fat in chipmunks. *J. Mammal.*, 47: 715—716.
13. Gaertner R. A., 1968: Seasonal variations in the energy budgets of the harvest mouse, *Reithrodontomys fulvescens*, and the cotton rat, *Sigmodon hispidus*. Ph. D. dissertation, Univ. of Arkansas, Fayetteville. 149 p.
14. Kenagy G. J., 1973: Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. *Ecology*, 54: 1201—1219.
15. Górecki A., 1965: Energy values of body in small mammals. *Acta theriol.*, 10, 23: 333—352.
16. Guthrie D. R., 1972: The effect of torpor on pulmo-cutaneous water loss in *Perognathus parvus*. Ph. D. dissertation, Univ. British Columbia, Vancouver, B. C.
17. Hayward J. S., 1965: The gross body composition of 6 geographic races of *Peromyscus*. *Canad. J. Zool.*, 13: 297—308.
18. Hsia-Wu-ping & Sun-Chung-lu, 1963: On the relative fatness of the red-backed vole, *Clethrionomys rutilus* Pall. *Acta Zool. Sinica*, 15: 33—43.
19. Hudson J. W., 1967: Variations in the patterns of torpidity of small homeotherms. [In: *Mammalian Hibernation III*, Ed., K. Fischer]: 30—46. American Elsevier Publ. Co., Inc., N. Y.
20. Iverson S. L., 1967: Adaptations to arid environments in *Perognathus parvus* (Peale). Ph. D. dissertation, Univ. British Columbia, Vancouver. 130 p.
21. Jameson E. W., Jr. & Mead R. A., 1964: Seasonal changes in body fat, water and basic weight in *Citellus lateralis*, *Eutamias speciosus* and *E. amoenus*. *J. Mammal.*, 45: 359—365.
22. Morhardt J. E., 1970: Body temperatures of white-footed mice (*Peromyscus* sp.) during daily torpor. *Comp. Biochem. Physiol.*, 33: 423—439.
23. Morhardt J. E. & Hudson J. W., 1966: Daily torpor induced in white-footed mice (*Peromyscus* sp.) by starvation. *Nature*, 212: 1046—1047.
24. Morton M. L. & Tung H. L., 1971: The relationship of total body lipid to fat depot weight and body weight in the Belding ground squirrel. *J. Mammal.*, 52: 839—842.

25. Myrcha A., 1968: Caloric value and chemical composition of the body of the European hare. *Acta theriol.*, 13, 5: 65—71.
26. Myrcha A., 1969: Seasonal changes in caloric value, body water and fat in some shrews. *Acta theriol.*, 14, 16: 221—227.
27. Panuska J. A., 1959: Weight patterns and hibernation in *Tamias striatus*. *J. Mammal.*, 40: 554—566.
28. Pearson O. P., 1960: The oxygen consumption and bioenergetics of harvest mice. *Physiol. Zool.*, 33: 152—160.
29. Pitts G. C., 1960: A study of gross body composition of small Alaskan mammals as compared with those from the temperate zone. Arctic Aeromedical Lab. Tech. Rep. 59—3. Ladd Air Force Base, Alaska. 28 p.
30. Pitts G. C., 1962: Density and body composition of the lean compartment and its relationship to fatness. *Amer. J. Physiol.*, 292: 445—452.
31. Pitts G. C. & Bullard T. R., 1968: Some interspecific aspects of body composition in mammals. [In: *Body composition in animals and men. Proc. Symp. Nat. Acad. Sci. Pub.*]: 45—70.
32. Pucek M., 1973: Variability of fat and water content in two rodent species. *Acta theriol.*, 18, 2: 57—80.
33. Sawicka-Kapusta K., 1968: Annual fat cycle of field mice *Apodemus flavicollis* (Melchior, 1834). *Acta theriol.*, 13, 19: 329—339.
34. Schreiber R. K., 1973: Bioenergetics of rodents in the northern Great Basin desert. Ph. D. dissertation, Univ. Idaho, Moscow, 146 p.
35. Scott I. M., Yousef M. K. & Bradley W. G., 1972: Body fat content and metabolic rate of rodents: desert and mountain. *Proc. Soc. Exp. Biol. and Med.*, 141: 818—821.
36. Sealander J. A., Jr., 1951: Survival of *Peromyscus* in relation to environmental temperature and acclimation at high and low temperature. *Amer. Midl. Nat.*, 46: 257—311.
37. Soholt L. F., 1973: Consumption of primary productivity by a population of kangaroo rats (*Dipodomys merriami*) in the Mojave Desert. *Ecol. Monogr.*, 43: 357—376.
38. Startin L., 1969: Body composition of the kangaroo rat (*Dipodomys merriami*). [In: C. C. Hoff and M. L. Riedesel eds., *Physiological systems in semiarid environments*]: 35—44, Univ. New Mexico Press, Albuquerque.
39. Tevis L., Jr., 1955: Observations on chipmunks and mantled squirrels in northeastern California. *Amer. Midl. Nat.*, 53: 71—78.
40. Willems N. J., 1971: Thermoregulation and water requirements in semiarid and montane populations of the least chipmunk, *Eutamias minimus*. Ph. D. dissertation, Univ. of Kansas, 101 p.
41. Yousef M. K. & Dill D. B., 1970: Physiological adjustments to low temperature in the kangaroo rat (*Dipodomys merriami*). *Physiol. Zool.*, 43: 132—138.
42. Yousef M. K. & Dill D. B., 1971: Responses of Merriams kangaroo rat to heat. *Physiol. Zool.*, 44: 33—39.

Accepted, November 23, 1974.

Environmental Sciences Division
Oak Ridge National Laboratory
P.O. Box X
Oak Ridge, Tennessee U.S.A. 37830
(Operated by Union Carbide Corporation
for the U.S. Atomic Energy Commission)

and

Biological Sciences
University of Idaho
Moscow, Idaho 83843 U.S.A.

R. Kent SCHREIBER i Donald R. JOHNSON

SEZONOWE ZMIANY SKŁADU CIAŁA I WARTOŚCI KALORYCZNE GRYZONI
GREAT BASIN

Streszczenie

Zbadano skład ciała i wartość kaloryczną u sześciu gatunków gryzoni pospolitych na pustyni Great Basin: *Perognathus parvus*, *Eutamias minimus*, *Peromyscus maniculatus*, *Reithrodontomys megalotis*, *Onychomys leucogaster*, *Dipodomys ordi*. Ogółem zbadano 920 osobników mierząc sezonowe (Ryc. 1—8) zmiany zawartości popiołu, tłuszczu, wody, masy beztłuszczowej i kaloryczności żywej wagi. Jakkolwiek gatunki aktywne cały rok różnią się nieco składem ciała od gatunków aktywnych tylko w określone sezony roku, to jednak różnice zwykle nie są istotne (Tab. 1—4, appendix). Zawartość popiołu waha się od 3,0 do 4,6% i nie wykazuje zależności ani od sezonu ani od gatunku. Udział wody zmienia się od 58,7 do 71,9% ciężaru ciała. Gatunki aktywne okresowo (*P. parvus*, *E. minimus*) wykazały istotne zmniejszenie zawartości wody przed popadnięciem w odrętwienie zimowe. Rehydracja wiosenna była związana ze zjadaniem zielonych roślin. Zawartość tłuszczu zmienia się znacznie, od 1,1 do 13,1% ciężaru całkowitego. Jesienna depozycja tłuszczu u *P. parvus* i *E. minimus* jest niewystarczająca jako zapas energetyczny na okres zimowy, ale może mieć ważne znaczenie jako izolacja na czas odrętwienia. Beztłuszczowa masa ciała stanowi 23,8 do 27,6% ciężaru ciała i podlega tylko niewielkim zmianom sezonowym. Jej kaloryczny ekwiwalent wynosi 4,50 do 4,89 kcal/g. Przedstawione zostały równania regresji opisujące zależności pomiędzy częściami składowymi ciała a jego ciężarem.

Ogólnie można stwierdzić, że kaloryczność świeżej masy ciała zależy wprost od ilości tłuszczu w organizmie a odwrotnie od jego uwodnienia. Średnia wartość roczna dla *P. parvus* wynosi 1,55 kcal/g, *O. leucogaster* — 1,61, *P. maniculatus* — 1,56, *R. megalotis* — 1,58. Odpowiednie wartości dla *E. minimus* (1,49) i *D. ordi* (1,39) zostały ustalone latem i jesienią (Tab. 1).

APPENDIX

Linear regression equations describing the relationship of body components to body weight in six species of desert rodents appear below. Data were grouped and analyzed to provide equations having the highest possible predictability. For all species, body water and lean dry content were positive linear functions of the body weight. Coefficients of determination (r^2) indicate a major part of the variability in these two body components was attributable to variation in body weight. Fat exhibited large individual differences and data best fit linear multiple regression equations incorporating body weight, water and lean dry composition. Regression coefficients indicate the effect, per unit change, of the independent variable (X) under consideration upon the dependent variable (Y).

Appendix Table 1

Seasonal relationships of body components in *Perognathus parvus*. Linear regression equations and correlation coefficients (r) for water (Y_W), lean dry (Y_{LD}) and fat (Y_F) compared to field weight (X_1). Equations for fat (Y_F) include coefficients for variation in other body components (X_2 =water, X_3 =lean dry weight). All correlation coefficients significant at 0.01 level.

Body component	Season	A d u l t			I m m a t u r e		
		Male	Gravid/lactating female ¹	Nongravid female ¹	Male ¹	Female ¹	
Y_W	Spring	$Y = 0.702X_1$ $r = 0.99$	$Y = 1.697 + 0.811X_1$ $r = 0.98$				
	Summer/ Fall	$Y = -0.737 + 0.739X_1$ $r = 0.97$	$Y = 0.659 + 0.744X_1$ $r = 0.98$	$Y = -1.523 + 0.796X_1$ $r = 0.96$	$Y = 1.388 + 0.591X_1$ $r = 0.93$	$Y = 1.577 + 0.566X_1$ $r = 0.96$	
Y_{LD}	Spring	$Y = 0.263X_1$ $r = 0.96$	$Y = 0.788 + 0.208X_1$ $r = 0.86$				
	Summer/ Fall	$Y = 0.260X_1$ $r = 0.92$	$Y = 0.259X_1$ $r = 0.82$	$Y = 0.452 + 0.234X_1$ $r = 0.91$	$Y = -0.684 + 0.306X_1$ $r = 0.93$	$Y = -0.955 + 0.338X_1$ $r = 0.97$	
Y_F	Spring	$Y = 0.926X_1 - 0.920X_2 - 0.932X_3$ $r = 0.96$	$Y = 0.374X_1 - 0.348X_2 - 0.372X_3$ $r = 0.73$				
	Summer/ Fall	$Y = 0.468X_1 - 0.391X_2 - 0.613X_3$ $r = 0.79$	$Y = 0.654X_1 - 0.604X_2 - 0.752X_3$ $r = 0.91$	$Y = 0.466X_1 - 0.388X_2 - 0.622X_3$ $r = 0.79$	$Y = 0.261X_1 - 0.200X_2 - 0.351X_3$ $r = 0.74$	$Y = 0.505X_1 - 0.414X_2 - 0.706X_3$ $r = 0.85$	

¹ Data combined for spring, summer and fall.

Appendix Table 2

Seasonal relationships of body components in adult *Eutamias minimus*. Linear regression equations and correlation coefficients (r) for water (Y_W), lean dry (Y_{LD}) and fat (Y_F) compared to field weight (X_1). Equations for fat (Y_F) include coefficients for variation in other body components (X_2 =water, X_3 =lean dry weight).

Body component	Season	Male	Female
Y_W	Summer	$Y=0.706X_1$ $r=0.93^{**}$	$Y=0.709X_1$ $r=0.96^{**}$
	Fall	$Y=6.680+0.451X_1$ $r=0.68^{**}$	$Y=3.719+0.555X_1$ $r=0.84^{**}$
Y_{LD}	Summer	$Y=1.395+0.298X_1$ $r=0.94^{**}$	$Y=-1.268+0.293X_1$ $r=0.96^{**}$
	Fall	$Y=0.253X_1$ $r=0.76^{**}$	$Y=2.358+0.184X_1$ $r=0.85^{**}$
Y_F	Summer	$Y=0.251X_1-0.224X_2-0.269X_3$ $r=0.75^{**}$	$Y=0.138X_1-0.088X_2-0.203X_3$ $r=0.52^*$
	Fall	$Y=0.030X_1-0.043X_2-0.105X_3$ $r=0.71^{**}$	$Y=0.030X_1$ $r=0.41^*$

* Significant at 0.05 levels, ** Significant at 0.01 level.

Appendix Table 4

Relationships of body components in three species of Great Basin rodents. Linear regression equations and correlation coefficients (r) for water (Y_W), lean dry (Y_{LD}) and fat (Y_F) compared to field weight (X_1).

Body component	Species	Male	Female	Combined sample
Y_W	<i>O. leucogaster</i>	$Y=0.665X_1$ $r=0.85^{**}$	$Y=-5.49+0.879X_1$ $r=0.95^{**}$	
	<i>R. megalotis</i>	$Y=1.189+0.553X_1$ $r=0.89^{**}$	$Y=0.670X_1$ $r=0.96^{**}$	
	<i>D. ordii</i>			$Y=0.697X_1$ $r=0.98^{**}$
Y_{LD}	<i>O. leucogaster</i>	$Y=0.244X_1$ $r=0.40^*$	$Y=2.44+0.143X_1$ $r=0.84^{**}$	
	<i>R. megalotis</i>	$Y=0.457+0.214X_1$ $r=0.89^{**}$	$Y=0.264X_1$ $r=0.92^{**}$	
	<i>D. ordii</i>			$Y=0.266X_1$ $r=0.96^{**}$
Y_F	<i>O. leucogaster</i>	$Y=0.050X_1$ $r=0.88^{**}$	$Y=0.790+0.011X_1$ $r=0.18$	
	<i>R. megalotis</i>	$Y=-0.512+0.088X_1$ $r=0.61^{**}$	$Y=0.041X_1$ $r=0.52^*$	
	<i>D. ordii</i>			$Y=0.021X_1$ $r=0.42^*$

* Significant at 0.05 level, ** Significant at 0.01 level.

Appendix Table 3
 Seasonal relationships of body components in *Peromyscus maniculatus*. Linear regression equations and correlation coefficients (r) for water (Y_W), lean dry (Y_{LD}) and fat (Y_F) compared to field weight (X_1).

Body component	Season	A d u l t			I m m a t u r e	
		Male	Gravid/lactating female	Nongravid female ¹	Male	Female
Y_W	Spring/summer	$Y = -1.058 + 0.698X_1$ $r = 0.97^{**}$	$Y = 0.671X_1$ $r = 0.94^{**}$	$Y = 0.647X_1$ $r = 0.86^{**}$	$Y = 0.653X_1$ $r = 0.90^{**}$	$Y = 0.672X_1$ $r = 0.97^{**}$
	Fall/winter	$Y = 0.657X_1$ $r = 0.98^{**}$	$Y = 0.668X_1$ $r = 0.97^{**}$			
	Spring/summer	$Y = 0.655 + 0.220X_1$ $r = 0.96^{**}$	$Y = 1.503 + 0.173X_1$ $r = 0.90^{**}$		$Y = 0.246X_1$ $r = 0.80^{**}$	$Y = 0.240X_1$ $r = 0.87^{**}$
Y_{LD}	Fall/winter	$Y = 0.252X_1$ $r = 0.95^{**}$	$Y = 1.106 + 0.184X_1$ $r = 0.91^{**}$	$Y = 0.249X_1$ $r = 0.85^{**}$		
	Spring/summer	$Y = 0.035X_1$ $r = 0.59^{**}$	$Y = -0.712 + 0.072X_1$ $r = 0.67^{**}$			
Y_F	Fall/winter	$Y = 0.031X_1$ $r = 0.37^{**}$	$Y = 0.029X_1$ $r = 0.51^{**}$	$Y = 0.040X_1$ $r = 0.09$	$Y = 0.033X_1$ $r = 0.52$	$Y = 0.398 + 0.070X_1$ $r = 0.78^{**}$

¹ Data combined for spring, summer and fall

* Significant at 0.05 level

** Significant at 0.01 level