Energy Flow Through a Population of Richardson's Ground Squirrels

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A mathematical model of energy flow was designed, and field data were gathered to determine the energetic role of Richardson's ground squirrel in its ecosystem from April 1974 to June 1976. Total energy flow decreased throughout the study period. Energy losses due to dispersal, weather or predation were greater in the summer of 1975 than in 1974. Losses during hibernation were less during the winter of 1975—76 than in the previous winter. The relationship of weather, predation and food supply to these changes is discussed. Daily energy budget (*DEB*) for an individual of mean weight (291.3 gm) was 35.49 kcal. *DEB* comprised 1) 4.08 kcal spent while above ground and not moving, 2) 4.48 kcal spent above ground and moving, and 3) 26.93 kcal spent in the burrow and not moving. Mean summer density decreased from 35.7/ha in 1974 to 29.9 in 1975. Density at arousal dropped from 25.0 in 1974 to 19.0 in 1975 to 15.4 in 1976. Possible mechanisms of population regulation are reviewed.

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I. INTRODUCTION

It is widely recognized that most of the energy flowing through an ecosystem passes through the detritus food chain without entering the grazing food chain. However, there remains much interest in and many unanswered questions concerning the role of small herbivorous mammals in temperate zone ecosystems (Golley *et al.*, 1975; Petrusewicz & Grodziński, 1975). Hence, as part of an effort to determine the role of Richardson's ground squirrel, *Spermophilus richardsonii elegans* (*S. elegans elegans, sensu* Nadler, Hoffmann & Greer, 1971) in a montane meadow ecosystem, we examined the energy flow through the population. Specifically, we attempted to devise a model illustrating this energy flow accurately and reliably.

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II. MATERIAL AND METHODS

1. Study Area

All laboratory and computer work in this study was conducted at the University of Colorado, Boulder, Colorado, U.S.A. Field work was performed at a site on the eastern slope of the Front Range of the Rocky Mountains at a location approximately 16 km southwest of Boulder (NE $\frac{1}{4}$ sec. 11 and NW $\frac{1}{4}$ sec. 12, T1S, R72W, Tungsten Quadrangle). Our study site of 3.6 ha was located in a gently sloping, bowl-shaped, approximately 76-ha meadow at 2440 m elevation. The site, grazed by horses, included both west- and south-facing slopes and several rocky outcrops.

The conspicuous plant taxa occupying the tract included *Poa* spp., *Bromus* spp.. *Iris missouriensis*, *Thermopsis divaricarpa*, *Helianthus annuus*, and *Helianthella quinquenervis*. The surrounding forests consisted mostly of stands of ponderosa pine (*Pinus ponderosa*), douglas fir (*Pseudotsuga menziesii*), and of lodgepole pine (*Pinus contorta*). A few, small stands of aspen (*Populus tremuloides*) were also in the vicinity.

2. Model Construction

Before other work began, a mathematical model of energy flow was constructed. Then values for the various model parameters were obtained from field, laboratory, and computer work. This model (Fig. 1) had two sections: 1) a model of energy
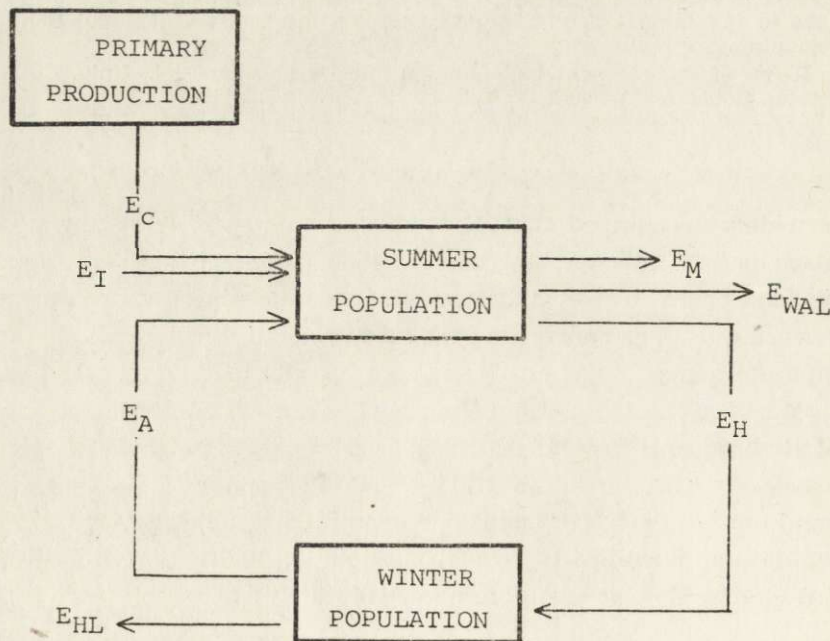

Fig. 1. Model of energy flow through a colony of Richardson's ground squirrels. *Spermophilus richardsonii elegans.* Symbols are defined in text.

flow during the active season, and 2) a model for the hibernating period. Energy flow during the active season was modeled by the following equation:

$$E_C + E_I + E_A = E_M + E_H + E_{WAL} \tag{1}$$

where E_C is the energy gained by the population via consumption, E_I is the energy gained from immigration, E_A is the energy within the population (*i.e.* in the body tissues of individuals) upon arousal from hibernation, E_M is the energy lost due to the collective metabolism of the individuals within the population during the active season, E_H is the energy within the bodies when hibernation begins, and E_{WAL} is the energy lost due to the loss of whole animals during the summer (*i.e.* loss via predation and dispersal).

Energy flow during hibernation was described by the equation:

$$E_H = E_A + E_{HL} \tag{2}$$

where E_H is the energy within the population when hibernation begins, E_A is the energy remaining in the population upon arousing for the next active season, and E_{HL} is the energy lost, due to metabolism and death, during hibernation. In general, data were gathered to directly determine all seven of the variables in equations 1 and 2 except that 1) E_C was determined by solving Equation 1 for E_C and 2) E_{HL} was determined by solving Equation 2 for E_{HL}.

Basic to the measurement of E_M is the daily energy budget (*DEB*) of the typical (*i.e.* average) individual. *DEB*, expressed as kcal/individual-day, is the number of kilocalories needed for maintenance during an average 24-hour period. In this study its measurement was slightly modified from that originally developed by G r o d z i ń s k i & G ó r e c k i (1967). The squirrels' day was divided into three components: 1) in the burrow and not moving, 2) above ground and not moving, 3) above ground and moving. Metabolic rates for each of these situations were calculated using the following equation proposed by W u n d e r (1975):

$$MR = \alpha(3.8W^{-0.25}) + 1.05W^{-0.50} \cdot [(38 - 4W^{+0.25}) - T_A] + (8.46W^{-0.40})V \tag{3}$$

where W is weight (in grams), T_A is ambient temperature (°C) and V is velocity (km/hr). Next, the time typically spent in each one of these activities was determined (see section on Field Techniques). The following equation was then used to calculate *DEB*:

$$DEB = (HR_M \cdot MR_M + HR_N \cdot MR_N + HR_B \cdot MR_B) W_M \tag{4}$$

where HR_M is the mean time (in hours) spent moving and above ground, MR_M is the metabolic rate estimated for the time spent moving above ground, HR_N is the mean time spent not moving and above ground, MR_N is the metabolic rate estimated for that time spent not moving and above ground, HR_B is the mean time spent in the burrow and not moving, and MR_B is the metabolic rate estimated for that time spent in the burrow and not moving.

Once *DEB* was calculated, E_M could be determined. The E_M equation:

$$E_M = X \underbrace{\sum_{i=1}^{N_M} DEB}_{(I)} + Y \underbrace{\sum_{i=1}^{N_{AF}} 0.61 \, DEB}_{(II)} \tag{5}$$

shows the energy loss to metabolism to be composed of two parts: (I) the loss due to the collective metabolism of all the individuals excluding losses due to

reproduction, where X is the length of the active season and M_M is the mean density and (II) the loss due to reproduction, where Y is the combined length of gestation and lactation and N_{AF} is the density of reproducing females. To calculate the metabolic cost of reproduction several assumptions were made: 1) reproduction was assumed not significantly to increase energy expenditure for males, 2) the increased expenditure for females was limited to the periods of gestation and lactation, and 3) this increased expenditure was similar to that of the only other rodents studied: *Clethrionomys glareolus. Mus musculus* and *Microtus arvalis*. G r o d z i ń- s k i & W u n d e r (1975) summarized the data for these three rodents and presented a mean percentage increase of 61⁰/₀ in respiration over non-reproducing females of the same body size. Therefore, the component (II) was used as a correction factor for the metabolic cost of reproduction.

3. Field Techniques

The field work was performed from April 1974 to June 1976. Information concerning density, survival, immigration, age and sex ratios, and weight as well as behavior and microclimate was necessary to test the model. Employing National live-traps (#201) baited with peanut butter, raisins and chopped apple, squirrels were trapped, marked and released throughout their active seasons. Each animal was uniquely marked with freeze-brands (H a d o w, 1972) and/or ear tags (National Tag Co. size #1). Each time a squirrel was captured, weight (to nearest 5 grams), total and tail length (to nearest 0.5 cm), age, sex, reproductive condition and identification number were recorded. Density (*i.e.* minimum number known to be alive) was determined by using computer programs provided by K r e b s (1972).

Survivorship was determined using a calendar of occurrence. In addition to capture-mark-recapture data, sightings for each individual were compiled on a weekly basis to determine the origin and fate of each individual.

Litter size was obtained in 1975 by counting the number in each litter during the four days after they first appeared above ground. This count is possible because litter mates group together and do not wander away from the nest burrow entrance during this time. The largest count for each of seven litters was used to determine a mean litter size.

Because wind, humidity, radiation and air temperature affect the thermal balance of an animal, operative environmental temperature, as developed by B a k- k e n (1976) and as applied to *S. richardsonii* by B y m a n (manuscript in prep.), was used as ambient temperature in Wunder's equation. To obtain operative environmental temperature the following data were gathered: 1) air temperature at the soil surface and at 200 cm above the surface, wind speed at 28 cm above soil surface, relative humidity, total sky and ground radiation and total solar short wave radiation. Because wind and radiation probably have negligible effects inside the animal's burrow, air temperatures obtained one meter down the tunnel from the entrance were used as ambient temperatures.

In addition the percentage of time spent above ground, the percentage of time spent moving when above ground, and running speed of the squirrels were obtained. Running speed was obtained by timing the movements of individuals among landmarks in the field. Likewise, the percentage of time spent above ground was determined on eight days during the summer of 1976. The number of minutes that an animal spent above ground was recorded for observation sessions which

lasted from 3.75 to 6.5 hours and encompassed all daylight hours. The percentage of time above ground was converted to the number of hours above ground during a 24-hour day. The percentage of time moving versus not moving was obtained from time budgets of the squirrels activities (Z e g e r s, 1977) obtained via metronome timing (W i e n s et al., 1970).

4. Laboratory Techniques

Fifteen individuals from the study area were sacrificed and brought into the laboratory. Each stomach-free carcass was dried and ground separately to a homogeneous mass in alcohol. Then, following standard chemical techniques and using a Labco Goldfisch Extraction Apparatus, lipid was extracted from three randomly selected, 3-gram samples of this material for each individual. Fat index (F. I.=grams fat/grams dry lean weight), percent fat, percent water, percent dry lean weight, and percent dry weight were obtained. In addition, one gram samples of the remaining homogeneous mixture were burned in Parr Oxygen-bomb Calorimeter to determine the caloric value of Richardson's ground squirrel tissue.

III. RESULTS

1. Field Data

Mean summer density, density at arousal, and density at hibernation were higher in 1974 than 1975 (Table 1). The number of animals lost

Table 1

Densities of *Spermophilus richardsonii elegans* in a montane meadow ecosystem. Units are number per hectare.

Season	Mean density, N	Range	Density at arousal N_A	Density at hibernation N_H	Density of reprod. females N_{AF}	Density of immigrants N_I	Density of animals lost during season N_{WAL}	Density of animals lost during following hibernation period, N_{HL}
Summer 1974	35.7	24—48	25.0	25.6	20.0	5.0	22.3	9.4
Summer 1975	29.9	19—49	19.0	15.4	16.0	5.8	33.1	0.0

during the summer (N_{WAL}) was greater in 1975 than 1974. In addition summer survivorship during 1975 was significantly less than that during 1974 ($\chi^2 = 16.98$, $p \leqslant 0.001$), although survivorship during the winter of 1975—76 was considerably greater than that during the previous winter ($\chi^2 = 12.35$, $p \leqslant 0.001$) (Table 2).

Mean litter size for 1975 was 5.9 (n=7; SD=1.57). This compares favorably with mean litter sizes of 3.7 to 8.0 in *S.r. richardsonii* (D o r r a n c e, 1975; N e l l i s, 1969), and with mean litter sizes of 5.9 and 7.0 for *S.r. elegans* (C l a r k, 1970; D e n n i s t o n, 1957).

Pooled data from all three summers gave mean live weight at arousal as 239.0 grams (n=42; SD=44.1), at the onset of hibernation as 296.0 grams (n=26; SD=51.1), and for the entire summer season as 291.3 grams (n=118; SD=77.2).

Table 2

Survivorship of *Spermophilus richardsonii elegans* in a Colorado montane meadow from 18 May 1974 to 19 June 1976. Ratios are the number known to be alive at the end of that season in a 1.39 hectare area divided by the total known to exist in that area during that particular season. Percentages are the percentages surviving at the end of that season.

	1974				1975			
	Summer		Winter		Summer		Winter	
	%	Ratio	%	Ratio	%	Ratio	%	Ratio
Adult males	77.78	7/9	42.86	3/7	30.77	4/13	100.00	4/4
Adult females	64.70	22/34	72.73	16/22	32.00	8/25	100.00	8/8
Juvenile males	37.50	3/8	33.33	1/3	33.33	3/9	100.00	3/3
Juvenile females	29.41	5/17	80.00	4/5	30.00	6/20	100.00	6/6
Total	54.41	37/68	64.86	24/37	31.34	21/67	100.00	21/21

The remaining data needed for computing *DEB* are summarized in Table 3. Mean velocity for moving ground squirrels was 5.5 Km/hr (range 0.47 to 32.4; SD=5.80; n=180); mean operative environmental

Table 3

Composition of daily energy budget (*DEB*=35.49 kcal/individual/day) of *Spermophilus richardsonii elegans*.

	Above ground; not moving	Above ground; moving	In burrow; not moving
Biomas (grams wet wg/indiv.)	291.3	291.3	291.3
Velocity (km/hr)	0.0	5.5	0.0
Air temp. (°C)	26.2	26.2	18.8
Metabolic rate (kcal/gm/hr)	0.00444	0.03075	0.00523
Time spent (hrs/day)	2.63	0.50	20.82
Energy expenditure (kcal/indiv./day)	4.08	4.48	26.93

temperature was 26.22°C (SD=13.12; n=30). Mean burrow temperature was 18.8°C (SD=3.409; n=84). On the average, 22.19% of a squirrel's time during daylight hours (*i.e.* 3.18 hr/day) was spent above ground. The squirrels were moving 15.65% of their time spent above ground (*i.e.* 0.5 hr/day).

2. Laboratory Data

Means of 32.7% dry weight, 66.8% water, 23.2% lean dry weight and 9.9% fat were obtained (Table 4). Caloric value of the tissue was 5.433 kcal/gm dry weight (range 4.974 to 5.998; SD=0.36; n=6).

Table 4

Body composition of free-living *Spermophilus richardsoni elegans* captured during the summers of 1975 and 1976 (n=15)

Body Component	Mean	Range	Standard Deviation
% dry wgt	32.7	23.9 —44.1	8.0
% water	66.8	76.1 —55.9	7.9
% lean dry wgt	23.2	34.6 —18.4	4.8
% fat	9.9	23.9 — 2.7	6.4
fat index	0.44	1.30—0.13	0.33

3. The Model

Total energy flow during the summer of 1975 (185,046.2 kcal/ha) declined from that of 1974 (216,659.0 kcal/ha). The values of all energy parameters decreased in 1975 from 1974 except the energy lost due to dispersal and death (E_{WAL}) which actually increased (Table 5). During

Table 5

Value for seven energy parameters of a population of *Spermophilus richardsonii elegans*. Units are kcal/ha. Symbols are defined in text.

Year	E_A	E_C	E_I	E_M	E_{WAL}	E_H	E_{HL}
1974	10570.3	203512.0	2576.0	191761.6	11491.6	13405.6	5372.0
1975	8033.4	174023.9	2988.9	159924.5	17057.5	8064.2	1552.9
1976	6511.3						

both summers most of the energy utilized was obtained by consumption (E_C equals 93.9% and 94.0% of total energy flow in 1974 and 1975 respectively) and lost via metabolism (E_M=88.5% and 86.4% of total flow in 1974 and 1975 respectively). E_{WAL} accounted for 5.3% and 9.2% of total energy flow. Only 6.2% of total flow in 1974 and 4.4% in 1975 was retained by the population as it entered hibernation (E_H). In 1974 E_A

accounted for 4.9⁰/₀; this was 4.3⁰/₀ in 1975. Immigration contributed the least to total flow, 1.2⁰/₀ in 1974 and 1.6⁰/₀ in 1975.

IV. DISCUSSION

1. Analysis of the Model

We devised a model of energy flow different from most other models of small mammal populations. Most energy flow models are based largely on a physiological analogy in which energy flow at the populational level is equated with that at the organismic level. Thus, a population has production, consumption, respiration, and assimilation as does the individual. Furthermore, O d u m's (1971) universal model of energy flow was designed to be applicable at the organismic, populational, and ecosystem levels.

Our model divides energy flow into different pathways. That values for all the energy parameters were obtained is evidence that the approach is possible. Moreover, exploitation efficiency and average daily metabolic rate ($ADMR$) derived from our model compare favorably with those determined, by more conventional techniques, for other small mammals. To compute exploitation efficiency ($E_C/F_a \times 100$) for *S. richardsonii* the food available (F_a) was equated with net primary production of temperate grassland (*i.e.* 2.556×10^7 kcal/ha, according to W h i t t a - k e r, 1975). The close agreement of this efficiency with those of other herbivores (Table 6) indicates the accuracy of the E_C value we obtained.

Table 6

Exploitation efficiencies for nine species of rodents.

Species	Exploitation Efficiency ($C/F_a \times 100$)	Reference
Clethrionomys glareolus and		
Apodemus flavicollis	0.6—1.9	Ryszkowski, 1969
Microtus agrestis	1.5—2.8	Hansson, 1971
M. oeconomus	.07	Gebczyńska, 1969
M. agrestis	2.9—13.7	Myllymaki, 1968
M. pennsylvanicus	0.4—1.6	Golley, 1960
M. agrestis and		
Pitymys subterraneus	1.03	Grodziński *et al.*, 1966
A. agrarius	0.14—0.31	Ryszkowski, 1969
S. richardsonii	0.68 & 0.79	This study

Since E_M is the dominant factor in computing E_C, errors in the value of E_M should be reflected in exploitation efficiency. In addition $ADMR$ calculated from our data is not statistically significantly different from

the *ADMR*'s of other rodents. Our *ADMR* lies within the 95% confidence interval for a 291.3 gram rodent predicted by the linear regression equation for body weight and *ADMR* presented by F r e n c h *et al.* (1976). The apparent accuracy of the exploitation efficiency and *ADMR* obtained from our data support the validity of our energy flow model.

2. Energy Flow in a Population of Richardson's Ground Squirrel

Our model discloses several interesting properties of energy flow in Richardson's ground squirrels, knowledge of which provides insight into the role of this squirrel in its montane meadow ecosystem. First, total energy flow during the summer of 1975 was only 85.4% of that in 1974. Several explanations are possible including decrease in food supply, changes in winter survivorship, and increased predation and/or disease. Decreased food supply seems unlikely. An admittedly subjective appraisal indicated that in 1975 the vegetation was thicker, lusher, and taller, with many more species blooming than in 1974. Weather conditions may account for this difference in primary production, although it also could be explained by reduced grazing pressure resulting from the decrease in numbers of squirrels in 1975. Climatological data for the Nederland, Colorado weather station (6 miles northwest of and at the same elevation as the study site) show the weather for each summer and its preceding winter to be essentially the same except that the summer of 1974 was cooler and much drier than that of 1975 (U.S. Dept. of Commerce 1974 and 1975). Precipitation from May through August was only 5.73 inches in 1974 compared to 9.03 in 1975. Indeed, May precipitation in 1974 was only 0.07 inch compared to 2.52 in 1975. Drought during May, critical in the growth of plants, undoubtedly was partially responsible for low primary production in 1974. Food supply may actually have been greater in 1975 than 1974.

Because survivorship data for the winter of 1973—1974 were not available, the possibility that changes in winter survivorship were responsible for the reduction in total energy flow was not testable. High surivorship over the winter of 1973—74 could have caused the higher arousal density of 1974 than of 1975. This difference could explain the greater energy flow in 1974 than in 1975. The difference in arousal energy (E_A), however, was only 2536.7 kcal, which was only 0.8% of the difference in total energy flow. Mean density, by affecting E_M, seemed to be the main factor causing the difference in total flow. Therefore, summer survivorship was probably more important in determining total flow than winter survival because mean summer density is more directly dependent on summer survival than on winter survival.

although winter survival certainly is critical in setting the starting density from which the population may expand.

If total energy flow does depend upon summer survivorship, then the importance of individuals lost to predators, disease, and dispersal (*i.e.* N_{WAL} and E_{WAL}) should have been greater in 1975 than 1974, and should have influenced the reduction in total flow in 1975. In fact, the relative importance of E_{WAL} to total flow did increase significantly in 1975 (from 5.3% to 9.2% of total flow) while the absolute energy flow increased from 11,491.9 kcal/ha in 1974 to 17,057.5 kcal/ha in 1975 (a 48% increase). This reflects an increase from 22.3/ha to 33.1/ha in number of squirrels lost (N_{WAL}) and corresponds to a decrease in summer survivorship from 54.4% to 31.3% (Tables 1 and 2).

The reduction in total energy flow was due, at least in part, to increased whole animal losses in 1975. Probably both predation (including road kills) and dispersal were involved. Unfortunately, we do not know the fates of those individuals that were lost from the population. Certainly some dispersed. Typically young males are the dispersing individuals. Q u a n s t r o m (1968) reported that 33 of 35 road kills were young males, which he presumed were dispersing. Y e a t o n (1969) found that juvenile males disperse farther than juvenile females. M i c h e n e r (1972) observed that no females moved more than 150 meters while 85% of young males and 100% of adult male movements ranged up to 450 meters. Dispersal, therefore, probably accounted for much of the loss of juveniles.

Predation also seems to affect summer survivorship. Although quantitative data were difficult to obtain, our observations indicate increased predation in 1975. Four instances of successful predation were recorded during 194 and 168 hours of observation in the summers of 1974 and 1975 respectively. All occurred in 1975 with two involving red-tailed hawks (*Buteo jamaicensis*) and two involving badgers (*Taxidea taxus*). In addition, badgers were observed in the study area on only one brief (15-minute) occasion in 1974, while they were observed on 17 days in 1975. Often they remained in the field, sunning or hunting, for 3—4 hours at a time. Hence, although avian predators were observed on 25 separate occasions in 1974 and on 20 in 1975, total predation pressure seems to have been greater in 1975 and could have accounted for increased E_{WAL} in 1975.

Another characteristic of energy flow was the decrease of E_H in 1975 to only two-thirds of what it was in 1974. In relation to total flow this represents a decline from 6.2% to 4.4%. This may have been due to increased E_{WAL} during 1975 (Table 5). Energy lost to dispersal and predators considerably reduced density at hibernation and thereby reduced

the energy available for hibernation. In a situation of this sort, immigration (E_I) should increase to fill the void. The observed increase of 412.2 kcal/ha in E_I was not enough, however, to compensate for the 5339.2 kcal/ha difference in E_H between 1974 and 1975. Because all factors pointed to greater availability of food in 1975 than 1974, food supply probably did not reduce E_H in 1975. Therefore, the decline in E_H appears to be due to 1) increased energy losses to dispersal and predation and 2) the inability of immigration to fill the resulting void. The population appears to have been below carrying capacity at hibernation time.

The difference in density at hibernation and the reduction in total energy flow from 1974 to 1975 calls attention to the problem of density regulation in Richardson's ground squirrel. Our results provide information which can be used to assess several hypotheses of population control. Although one factor alone seems unlikely to regulate density, exploring the possible impacts of several factors on density in light of the information generated from the model is worthwhile.

The role of predators in regulating densities of small mammals is controversial (*e.g.* K r e b s & M y e r s, 1974). To determine the full interaction between one population of predators and one population of its prey is nearly impossible. Predation is difficult to observe, while food webs are complex and causes of death are many; hence the impact of the predator is obscured. However, predation does seem to reduce populations in peak phase and to hold density at low phase delaying the next increase phase (K r e b s & M y e r s, 1974). Our population of Richardson's ground squirrels declined from 1974 into the spring of 1976 (Table 5). Possibly predation played an important role in density regulation during that decline. Certainly, as we have noted, the visibility of badgers increased in 1975. Also, the low density of squirrels at arousal in 1976 (15.4/ha compared to 25/ha in 1974) could have been due to heavy predation by badgers the previous summer.

Another hypothesis regarding density control is the effect of weather. B a r a s h (1974), F u l l e r (1969), and M e r r i t t & M e r r i t t (in press) presented evidence that weather does influence the density of rodents. Weather certainly could affect the density of *S.r. elegans*. More favorable snow and temperature conditions during the winter of 1975—76 compared to the previous winter could have increased survivorship, thereby modifying breeding density and the potential for increase within the population. However, we found no statistically significant differences between the means of the monthly values for mean temperature, mean minimum temperature, degree days, total precipitation, or maximum snow depth (U.S. Dept. of Commerce 1975 and 1976). No data are

available, unfortunately, on the frequency or severity of thaws and of snow-free periods, both of which are critical in assessing the harshness of the winter for hibernating animals.

Spring weather may also affect density by influencing reproductive success. Z e g e r s & W i l l i a m s (1977) found fat levels (energy reserves) nearly depleted for adult male Richardson's ground squirrels and completely depleted for adult females during the first month after arousal in 1976. M o r t o n (1975) documented a similar situation for *S. beldingi*. Possibly this condition was caused by the energetic costs of reproduction and the minimal supply of food. M i c h e n e r (1973) correlated arousal and breeding with increasing daily maximum temperature in late March and early April for *S.r. richardsonii*. If unseasonably cool spring temperatures delay emergence, and hence breeding, the increased length of hibernation may deplete fat reserves to the point where the energetic costs of reproduction could result in the death or decreased fertility of some individuals.

Another factor influencing density is social interaction. Behavior has been identified as the important density regulating factor for other populations of ground squirrels. Territoriality among breeding females and dispersal of young appear to be dominant regulators for the Arctic ground squirrel (C a r l 1971) and the Uinta ground squirrel (S l a d e & B a l p h, 1974). Dispersal of young appears to produce a significant reduction in the number of potentially breeding individuals (M i c h e-n e r, 1972; Y e a t o n, 1969). Hence, social organization may inhibit increases in density. Moreover, social organization appears plastic enough to allow population increase when density is low (B a r a s h, 1974; D o r r a n c e, 1975; S l a d e & B a l p h, 1974). Therefore, although our model gives no information concerning social interaction as a density-regulating mechanism, data from other populations of sciurids suggest that this is likely to be the case.

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PRZEPŁYW ENERGII PRZEZ POPULACJE *SPERMOPHILUS RICHARDSONII ELEGANS*

Streszczenie

Na podstawie badań terenowych określono energetyczną rolę *Spermophilus richardsonii elegans* (K e n n i c o t t, 1863) w ekosystemie, od kwietnia 1974 do czerwca 1976. W tym celu opracowano także matematyczny model przepływu energii (Ryc. 1). Stwierdzono, że przepływ energii uległ zniżeniu w okresie badań. Straty energii wynikające z emigracji, warunków pogodowych lub drapieżnictwa były latem 1975 większe niż w tym samym sezonie 1974 roku. Natomiast takie same straty w okresie hibernacji były niższe zimą 1975/76 niż straty zanotowane poprzedniej zimy (Tabela 2). Przedyskutowano zależności między warunkami pogodowymi, drapieżnictwem, zasobnością pożywienia a przepływem energii (Tabela 5).

Dobowy budżet energetyczny (Tabela 3) dla osobnika o średnim ciężarze ciała wynoszącym 291,3 g wynosi 35,49 kcal. Składa się nań: (1) 4,08 kcal wydatkowanej w czasie spoczynku poza gniazdem, na powierzchni gleby, (2) 4,48 kcal wydatkowanej w okresie ruchliwości na powierzchni, (3) 26,93 kcal zużytkowanej w okresie spoczynku w gnieździe.

Średnia liczebność gryzoni wynosiła latem 35,7 osobnika/ha w 1974 roku i zniżyła się do 29,9 osobnika/ha w 1975 r. Liczebność zwierząt w okresie budzenia się ze snu zimowego zniżyła się z 25,0 osobników w 1974 roku do 19,0 w 1975 roku i 15,4 w 1976 r. (Tabela 1). Omówiono także potencjalne mechanizmy regulacyjne działające w populacji tego gatunku.