

Energy Requirements and Diet of the California Ground Squirrel Author(s): Frank Schitoskey, Jr. and Sarah R. Woodmansee Source: *The Journal of Wildlife Management*, Vol. 42, No. 2 (Apr., 1978), pp. 373-382 Published by: <u>Wiley</u> on behalf of the <u>Wildlife Society</u> Stable URL: <u>http://www.jstor.org/stable/3800273</u> Accessed: 30/10/2014 17:33

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Wiley and Wildlife Society are collaborating with JSTOR to digitize, preserve and extend access to *The Journal* of Wildlife Management.

http://www.jstor.org

# ENERGY REQUIREMENTS AND DIET OF THE CALIFORNIA GROUND SQUIRREL

FRANK SCHITOSKEY, Jr., U.S. Fish and Wildlife Service, Denver Wildlife Research Center, Denver, Colorado 80225<sup>1</sup> SARAH R. WOODMANSEE, 1321 Lynnwood, Fort Collins, Colorado 80521

Abstract: Oxygen requirements of the California ground squirrel (Spermophilus beecheyi fisheri) are 0.75 ml/g/h. A ground squirrel's daily maintenance requirements are 92.40 cal/g/day. Ground squirrels absorbed 83 percent of the dry matter in forage and 91 percent of the dry matter in oat groats. Forbs other than legumes were the most prevalent forage plants on the study area. Although legumes made up over 50 percent of the ground squirrel's diet in March and April, nonlegume forbs were the major part of the animal's diet. A ground squirrel population of 8.4/ha required in February, March, and April as estimated 0.6, 0.4, and 0.2 percent, respectively, of the forage plants available. During the green forage season, ground squirrels and cattle feed largely on different plant species.

J. WILDL. MANAGE. 42(2):373-382

The California ground squirrel traditionally has been considered a serious pest on annual-plant rangeland (Grinnell and Dixon 1918, Fitch and Bentley 1949, Howard et al. 1959) and millions of acres are treated annually in California with various toxicants to suppress its populations. Justification for control often is based on work conducted at the San Joaquin Experimental Range, Madera County, California by Fitch and Bentley (1949) and Howard et al. (1959). They suggested that the California ground squirrels competed with livestock primarily during the green forage season. At the San Joaquin Experimental Range we studied energy relationships in a population of S. b. fisheri during the green forage season and conducted diet studies throughout the vear.

This paper reports on work supported in part by National Science Foundation Grants GB-31862X2 and GB-42133X to the Grassland Biome, U.S. International Biological Program (IBP) for "Analysis of Structure, Function, and Utilization of Grassland Ecosystems." We thank R. Hubbard and D. A. Duncan of the Pacific Southwest Forest and Range Experiment Station, U.S. Forest Service, for space and invaluable assistance at the San Joaquin Experimental Range. Duncan also furnished primary production data used in this study.

# STUDY AREA

The San Joaquin Experimental Range is located near Coarsegold, Madera County, California, in the Sierra Nevada foothills on the east side of the San Joaquin Valley. The area is gently rolling with elevations between 215 and 520 m. Seasonal variability of weather affects quality, time of growth, and quantity of the vegetative cover. Growth of vegetation reaches its maximum during the spring and is followed by little or no growth in the summer, some in the fall, and very little growth during the winter (Talbot and Biswell 1942).

# METHODS

#### **Energy Requirements**

Oxygen consumption was measured on 26 adult squirrels that had been held in the laboratory 1 to 4 days, but had not been fasted. Air was moved through the open respirometer system at a rate of 200

<sup>&</sup>lt;sup>1</sup> Present address: South Dakota Cooperative Wildlife Research Unit, South Dakota State University, Brookings 57007.

ml per minute,  $O_2$  consumption was measured with a polarographic oxygen analyzer and readings converted to standard temperature and pressure. The system was operated for 1 hour at ambient temperature (25–28 C) before readings were made; the lower critical temperature for *S. b. beecheyi* lies between 20 and 25 C; upper critical temperature is above 30 C (Baudinette 1972). Readings then were made at 10-minute intervals until the same reading was obtained 4 successive times.

To confirm reliability of resting metabolic rate estimates, individual energy requirements of 20 adult ground squirrels (12 females and 8 males) were calculated from the results of oxygen consumption studies. Animals were maintained on a diet consisting of this amount of energy, in the form of oat seeds for 14 days. Daily rations were calculated by determining the dry matter digestion efficiency of squirrels on an oat diet and assuming a 19 percent loss in conversion of digested energy to metabolized energy (Harris 1971). Food consumption was checked daily. Animals were weighed at the beginning and end of the test, and weights compared with a paired *t*-test (Steel and Torrie 1960:78).

#### Assimilation Efficiency

Ash content of feed and feces may be used as an indicator of assimilation efficiency, if the amount of ash absorbed is known (Johnson and Groepper 1970, Soholt 1973). We used the ash tracer technique (Soholt 1973) to determine assimilation efficiencies for 14 adult males and 15 adult pregnant females collected the first week of April 1973. Contents of the stomach and rectum were removed, weighed, dried to constant weight at 60 C for 48 h, reweighed and analyzed for ash, crude protein, fat, and fiber. In addition, to determine the amount of ash digested 10 male and 10 female squirrels were fed only oat groats for 5 days. Later, the same animals were fed only alfalfa pellets for 5 days. Animals were offered water ad libitum. Samples of the grain and feces were collected daily, dried, and analyzed.

All dried materials were sent to Industrial Laboratories, Inc., Denver, Colorado, for proximate analysis. They used standard procedures to determine ash, crude protein, fat, and fiber (Horwitz 1970). Nigrogen-free extract was determined by difference (Morrison 1956:14). We used data from proximate analysis to determine caloric content of food items.

# Diet

Using techniques described by Cavender and Hansen (1970), we determined the diets of 423 California ground squirrels collected monthly (except for December 1972) from November 1972 through February 1974. Five slides were made from each stomach and 20 random fields were read from each slide. Information on forage availability was obtained from unpublished IBP studies in which 12, 0.5-m plots were clipped in grazed pastures on native annual rangeland. Clipped samples were dried, weighed, separated, and identified as Bromus spp., Festuca spp., Erodium spp., Trifolium spp., Lotus Purshianus, miscellaneous legumes, miscellaneous forbs, and miscellaneous grasses.

#### RESULTS

#### **Energy Requirements**

The mean oxygen requirement of resting adult squirrels, within their thermoneutral zone, was 0.75 ml per gram of live body weight per hour (N = 26, SD =

0.21). There was no significant difference (P > 0.01) between sexes. Assuming the caloric equivalent of oxygen to be 4.7 kcal/l (Kleiber 1961:126), the resting metabolic rate of the California ground squirrel is 3.52 cal/g/h or 84.48 cal/g/day.

Squirrels required 118.2 cal/g/day when on an exclusive oat-groat diet because they digested 91 percent of the dry matter in oat groats and lost another 19 percent in metabolism (Harris 1971); thus, their gross energy requirement was 1.4 times their net energy requirement. Squirrels invariably consumed all of their daily rations. Mean weight at the beginning of the test was 505 g (SD = 63), mean weight at termination was 498 g (SD = 62). There was no significant difference (P > 0.01) between paired beginning and termination weights.

### Assimilation Efficiency

Squirrels absorbed 22 percent of the ash in oat groats and 60 percent of the ash in alfalfa pellets. From the groats they assimilated 91 percent of the dry matter, 83 percent of the protein, 83 percent of the fat, 57 percent of the fiber, and 96 percent of the nitrogen-free extract. The groats contained 2 percent ash, 16 percent protein, 6 percent fat, 2 percent fiber, and 73 percent nitrogen-free extract.

# Diet

Forbs, other than legumes, were the most prevalent forage plants on the study area and in the diets of squirrels. Filaree (*Erodium* spp.) leaves and seeds formed more than 15 percent of the diet during 10 of the 15 sampling periods (Table 1). Nonlegume forbs formed 35 percent or more of the monthly diet in every period except November 1972 and August 1973 when acorns and grasses formed 56–78 percent of the diet, and in March and April, when legumes formed 50–63 percent of the diet. Legume leaves made up 30 percent of the diet in February, 50 percent in March, and 63 percent in April. Grasses composed 5 percent or more of the squirrel diet in every sampling period but one. Grasses were more prevalent during the fall and early winter than any other period. Ground squirrels consumed arthropods during every sampling period but 2; amounts ranged from traces to a high of 4 percent in May.

#### DISCUSSION

### **Energy Requirements**

We determined the resting oxygen requirement of the California ground squirrel to be 0.75 ml/g/h. While inactive, the California ground squirrels require 3.52 cal/g/h to maintain normal physiological functions without weight loss. Ground squirrels spend much of their time in the burrow system (Fitch 1948) where they are protected from wind, rain, and adverse temperatures (Baudinette 1972). They restrict their active periods to the milder parts of the day, thus conserving energy for needs other than thermoregulation.

Ground squirrels are active primarily at midday in the fall, winter, and early spring (Fitch 1948:548). Although squirrels may spend as much as 7 hours above ground during the green forage season, they seldom spend more than 3 hours foraging; the rest of the time above ground is spent resting. We do not know how much time they spend digging, but there was probably little in the study area because the colonies there are old. We presumed that during the spring squirrels regulate their activity so that they are not exposed to temperatures outside their thermoneutral zone. We assumed that ground squirrels were active 4.5 h/day to allow for additional above and below

Plants	Nov (28)	Jan (12)	Feb (30)	Mar (30)	Apr (34)	May (36)	Jun (32)	Jul (19)	Aug (24)	Sep (31)	Oct (22)	Nov (34)	Dec (21)	Jan (40)	Feb (30)
Grasses:															
Bromus spp.	17	10	3	2	1	4	9	9	$15^{\rm a}$	14	35	19	28	14	13
Festuca spp.	1	2	2	1	1	tr <sup>b</sup>	tr	tr	$1^{a}$	1	1	2	2	2	
Hordeum spp.	4		tr	1		1	1	tr	tr						
Poa spp.		1	1	tr		tr	tr	tr		tr	tr	3	5	3	1
Legumes:															
Lotus spp.			2	tr	1	tr				tr		3	tr		2
Lupinus spp.		12	17	27	32	10	3		tr	2	tr	1	3	11	14
Medicago hispida			5	4	10	1	tr	<b>4</b>	$3^{a}$	6		tr	4	2	tr
Trifolium ciliolatum	2	10	3	4	4	2					tr			tr	tr
Trifolium microcephalı	ım	tr	3	15	10		1	9	1					tr	7
Trifolium obtusiflorum		1	tr		6	8	9								
Forbs:															
Amsinckia spp.		7	5	2	5	2	2	tr	tr	tr	6	12	15	13	30
Baeria spp.		2	3	2		tr	tr				tr			tr	tr
Brodiaea spp.	2	10	1	1	1	tr									tr
Calandrinia ciliata		5	7	3	3	1	tr	tr	tr	tr	tr	tr	tr	1	
Eremocarpus setigerus	1	tr		1	tr		tr	tr	tr	6	3	tr	tr	tr	tr
Erodium spp. veg.	2	32	21	10	8	6	17		tr		12	24	17	32	13
Erodium spp. seed						6	19	59	25	24	4	4	tr	1	
Eriogonum spp.	tr	2	4	1	tr	3	15	5	1	1	tr	1	2	1	1
Holocarpha Heermanni	i 8		2	1		14	14	1	1	$13^{-1}$	10	9	tr	1	
Plagiobothrys spp.	1	2	4	3	6	16	tr	_	tr			tr	tr	tr	1
Silene gallica	-	8	1	6	6	4	3	tr			tr		2	1	6
Trees and shrubs:															
Quercus spp. seed	56	6	10	3	1	3	3	8	40	27	22	21	20	16	5
Arctostaphylos maripos				6	-	tr	tr					tr			-
Miscellaneous:															
Arthropods	2	tr	tr	tr	2	4	2	tr	3	3	3	tr		tr	
Moss & lichens	2	-	tr			tr	tr	0	tr	tr	tr		tr	tr	tr

Table 1. Composition (mean percentage of food items) of monthly diets of the California ground squirrel. Samples collected from November 1972 through February 1974; sample sizes in parentheses.

<sup>a</sup> Seed. <sup>b</sup> tr = < 1%.

ground movements. We can assume that they have an active period of 4.5 h/day with a metabolic rate of 1.5 times resting metabolic rate (Yousef et al. 1973) and 19.5 h/day at resting metabolic rate. Thus, a squirrel's daily net energy requirements for maintenance would be

(19.5 h) (3.52 cal/g/h) + (4.5 h)(3.52 cal/g/h) (1.5) = 92.40 cal/g/day (1)

In the winter and spring there is little or no growth or fat deposition in ground squirrels, nor do they engage in a significant amount of work (Fitch 1948). The primary form of production energy required by ground squirrels at this time of the year is for reproduction and lactation. Most female ground squirrels are pregnant during the spring. Fitch (1948:567) noted that breeding occurred from late January until early March. The earliest pregnancy we found was 25 January 1973. In February, 3 of 13 females examined were pregnant; in March, 19 of 29 females were pregnant, 4 lactating, and 6 neither: and in April, 9 of 29 females taken were pregnant, 17 lactating, and 3 neither. For calculating daily net energy requirements, we assumed that no females were pregnant in January; that 25 percent were pregnant in February; that 66 percent

were pregnant and 14 percent lactating in March; and that 30 percent were pregnant and 70 percent lactating in April.

Gestation is approximately 30 days in the California ground squirrel (Grinnell and Dixon 1918) and young are not fully weaned until at least 55 days old (Fitch 1948:580, Tomich 1962:266). Thus, young do not depend on leafy vegetation to any significant degree until late April or early May, after the peak of the green forage season and also during the period that adult squirrels are consuming seeds. Therefore, we ignored the contribution of young animals to forage removal.

Pregnancy increases energy needs by 13.5 to 24.5 percent in dairy cattle (Flatt et al. 1969:134), by 32 percent in Microtus arvalis (Migula 1969), and by 24 percent in Clethrionomys glareolus (Kaczmarski 1966). If we assume an increase in net energy needs of 25 percent for pregnancy in ground squirrels, the daily resting energy requirement of a pregnant female would be 115.5 cal/g/day. Energy requirements for lactation have been reported to be 100 percent greater than maintenance energy requirements in Peromyscus maniculatus (Johnson and Groepper 1970:176). On this basis, the resting energy requirements for a lactating ground squirrel would be 184.8 cal/g/day.

During the green forage season, the average body weight is 662 g for males and 508 g for females (Fitch 1948). Fitch (1948:582) found that the average density of ground squirrels was 8.4/ha on his 32.4-ha study site, which he considered a higher than average population. Estimated population density on our area varied between 7.7 and 9.4 squirrels per hectare over a 5-year period. Fitch's population studies were more detailed than ours and included estimates of sex ratios; therefore, we chose his data for our model. Because Fitch's population was 45 per-

cent males, there was an average of 3.9 males and 4.5 females per hectare. Based on these figures, the daily net energy demand by ground squirrels on the San Joaquin Experimental Range would be approximately 449.8 kcal/ha/day in January (Table 2), 461.3 kcal/ha per day in February, 508.2 kcal/ha per day in March, and 610.9 kcal/ha per day in April. Thus, peak energy demands during the green forage season coincide with peak forage production.

### Assimilation Efficiency

We calculated that the assimilation efficiency of California ground squirrels was 83 percent for foliage. This is similar to the 79.9 to 84.5 percent efficiencies reported for *Spermophilus richardsonii* and other rodents by Johnson and Groepper (1970:541), and is also similar to the 85 percent efficiency assumed for rodents by Harris (1971:235). However, under laboratory conditions California ground squirrels were able to assimilate 91 percent of the dry matter in seeds.

Harris (1971:235) reported a 10 percent loss in the conversion of digestible energy to metabolized energy, and another 10 percent loss in the conversion of metabolizable energy to net utilizable energy. Using these figures, we calculated that the overall energy conversion efficiency of an adult California ground squirrel on a foliage diet would be

$$(0.83)(0.90)(0.90) = 0.67$$
 (2)

The overall conversion efficiency of an adult ground squirrel on a seed diet would be

$$(0.91)(0.90)(0.90) = 0.74$$
 (3)

While feeding on foliage, an adult ground squirrel would require 1.5 times its energy needs to make up for losses in con-

Sex and reproductive status		No	./ha		Net energy requirement (kcal/ha/day)					
	Jan	Feb	Mar	Apr	Jan	Feb	Mar	Apr		
Males	3.90	3.90	3.90	3.90	238.6	238.6	238.6	238.6		
Females: Nonreproductive	4.50	3.38	0.90		211.2	158.7	42.3			
Pregnant Lactating		1.12	$2.97 \\ 0.63$	$1.35 \\ 3.15$		64.0	168.2 59.1	$76.5 \\ 295.8$		
Total	8.40	8.40	8.40	8.40	449.8	461.3	508.2	610.9		

Table 2. Estimated daily net energy requirements for a population of 8.4 California ground squirrels per hectare during the green forage season.

version inefficiencies; while on a seed diet, it would require 1.4 times its daily energy needs.

There has been much controversy about how much forage a California ground squirrel consumes. Grinnell and Dixon (1918:636) estimated that 200 squirrels consumed as much as 1 steer and that daily intake was approximately 28 g (dry weight) per squirrel. Fitch (1948:521) estimated that daily intake was 31 to 49 g. We estimate that an average, adult male California ground squirrel weighing 662 g would require 61.17 kcal per day and would have a forage conversion efficiency of 0.67. Thus, such an animal would require a daily intake of 91.30 kcal of forage.

$$(1/0.67)(61.17) = 91.30$$
 kcal (4)

The April diet of the California ground squirrel had an average caloric value of 4.65 kcal/g. Assuming the caloric value of foliage diets to be constant, an adult male ground squirrel would require the intake of 19.6 g of dry matter per day during the green forage season. During the same period, an adult female weighing 508 g would require approximately 15.0 g/day if nonreproductive, 18.8 g/day if pregnant, and 30.0 g/day if lactating.

When seeds are available for consumption, the total weight of food required by squirrels is reduced. Because the conversion efficiency for seeds is 0.74, the daily requirement for a 662-g adult male ground squirrel on an all seed diet would be approximately 82.65 kcal.

$$(1/0.74)(61.16) = 82.65$$
 kcal (5)

This amount would be furnished by approximately 16.3 g of dry seed, assuming that seed contains 5.06 kcal/g (Golley 1961:582).

Feeding on seeds would be the best strategy for the California ground squirrel from an energetic standpoint. They can digest seeds more efficiently than foliage. Seeds contain more energy (5.06 vs. 4.65kcal/g), and seeds contain less moisture (10 vs. 75%+). However, the squirrels may need the additional moisture from foliage to maintain water balance. In addition, the diet patterns suggest that either seeds are not available during the green forage season, or the squirrels cannot locate them under the dense mat of green forage.

#### Forage Requirements

Dry-weight composition of herbivore diets may be estimated from the results of microscopic analysis of diet samples (Sparks and Malechek 1968). Free et al. (1970) demonstrated that food plants composing more than 5 percent of esophageal samples from steers, fecal samples from steers, and fecal samples from sheep fed

		February			March		April			
Plant	kg/ha required <sup>a</sup> (a)	kg/ha avail. <sup>b</sup> (b)	% of avail. required (100·a/b)	kg/ha required <sup>a</sup> (a)	kg/ha avail. <sup>b</sup> (b)	% of avail. required (100· <i>a/b</i> )	kg/ha required <sup>a</sup> (a)	kg/ha avail. (b)	% of avail. required $(100 \cdot a/b)$	
Bromus spp.	0.12	93	0.1	0.10	160	0.1	0.06	320	tr <sup>d</sup>	
Festuca spp.	0.08	73	0.01	0.05	132	tr	0.06	556	tr	
Misc. grasses <sup>c</sup>	0.04			0.05	2	2.5		20		
Lotus Purshianus	0.08	1	8.0		27		0.06	158	tr	
Trifolium spp.	0.25	49	0.5	0.97	96	1.0	1.18	314	0.4	
Misc. legumes <sup>c</sup>	0.92	11	8.4	1.57	27	5.8	2.48	66	3.8	
Erodium spp.	0.87	174	0.5	0.51	275	0.2	0.47	736	0.1	
Misc. forbs <sup>c</sup>	1.12	336	0.3	1.02	684	0.2	1.24	1.573	0.1	
Other foods	0.42			0.46			0.18	_,		
Unknown	0.26			0.35			0.24			
Total foliage	4.16	738	0.6	5.08	1,404	0.4	5.91	3,746	0.2	

Table 3. Estimated requirements for various food plants by a population of 8.4 California ground squirrels per hectare, and amounts of these plants (standing crop biomass) available on study plots.

<sup>a</sup> Kg/ha, dry weight, required by squirrels each month, based on calculated total food requirement and the percentage distribution of feed items in the diet (Table 1, 1973 figures).
<sup>b</sup> Kg/ha dry weight of plant biomass, based on 12 samples clipped from 0.5-m plots each month, 1973.
<sup>c</sup> "Miscellaneous" grasses, legumes, and forbs were those not identified to species from clipped plant samples; for calculating squirrel food requirements, "miscellaneous" was considered to represent all species listed in Table 1 but not here.

on the esophageal samples, could be identified and quantified using techniques similar to those we used.

Food requirements were estimated by assuming that a squirrel population of 8.4/ ha required a total of 450 kcal/ha per day in January, 461 kcal/ha per day in February, 508 kcal/ha per day in March, and 611 kcal/ha per day in April (Table 2). We assumed that the energy content of the diet was 4.65 kcal/g and that the overall energy conversion efficiency was 67 percent, so that squirrels would have to consume 1.5 times their daily requirement to make up for the losses in digestion and metabolism. We used these data to calculate monthly food requirements for each group of plants found in the diet, and compared these with the production (biomass available) for each group (Table 3).

In January (31 days), ground squirrels required 20,925 kcal/ha, or 4.5 kg/ha, but we have no forage production figures for January. The total gross energy requirement for the 28 days of February was 19,362 kcal/ha; therefore, squirrels required 4.16 kg/ha of forage to provide this requirement.

# (28 days)(461 kcal/ha/day)

### (1.5)/(4.65 mcal/kg) = 4.16 kg/ha (6)

In February, the squirrel population on our study area required 4.16 kg/ha of foliage, and production in mid-February was 738 kg/ha. In March, when squirrel requirements were 5.08 kg/ha, production was 1,404 kg/ha. In April, when squirrel foliage requirements were 5.91 kg/ha, production was 3,746 kg/ha. In other words, squirrel requirements were 0.6 percent of what was available in February, 0.4 percent of what was available in March, and 0.2 percent of what was available in April. Thus, even if ground squirrels destroyed 10 times what they consumed, as reported by Fitch and Bentley (1949:317), they would destroy 6.0, 3.6, and 1.6 percent, respectively, of what was available in February, March, and April.

Fitch and Bentley (1949:308) stocked a 0.2-ha enclosure with 6 adult male ground squirrels, a number they considered to be 8 times the average concentration on surrounding rangeland. They considered the average adult density on rangeland, before birth of young, to be

3.7/ha. Grinnell and Dixon (1918:636) arrived at a similar population estimate. From their enclosure studies, Fitch and Bentley (1949:309) estimated that 1 adult ground squirrel eliminated, through all activities, 41 kg (green weight) of forage during the green forage season. Using their estimate of 3.7 squirrels/ha, the total amount of green forage removed by ground squirrels would have been approximately 152 kg/ha. Assuming the plants to be 75 percent moisture, this would be 38 kg/ha dry weight. Average vearly production on their study site (counting what squirrels destroyed) was 3,499 kg/ha (dry weight) in the squirrel enclosure. Thus, squirrels destroyed 3.3 percent of annual standing crop biomass at peak of production.

Fitch (1948:525) estimated that a California ground squirrel population of 3.7/ ha would consume an average of 7.8 kg/ ha of green forage a month, or 2.0 kg/ha dry weight. Thus, ground squirrel consumption averaged 12 kg/ha (dry weight) during the 6-month growing season. Assuming an annual production of 3,499 kg/ ha, ground squirrel consumption would have been 0.3 percent of production. Even though squirrels consume only a small part of forage production, Fitch and Bentley (1949:321) concluded that ground squirrels destroyed 35 percent of the herbage crop.

Howard et al. (1959) studied differences in heifer weight gains on squirrelinfested and squirrel-free pastures. They concluded that the 12 heifers weighing 235 kg on a squirrel-free plot gained an average of approximately 0.5 kg per day more than the 12 heifers in a pasture with 9.4 squirrels per hectare. They attributed the lack of gain to competition with squirrels.

The small degree of competition between ground squirrels and livestock may

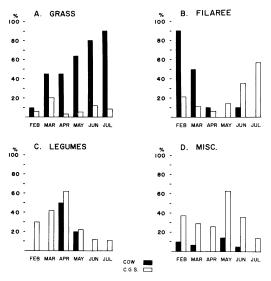


Fig. 1. Seasonal variation of percentage composition of plants in the diets of California ground squirrels (C.G.S.) and cows on the San Joaquin Experimental Range. Data on cow diets from Wagnon (1963).

be demonstrated by comparing the diets of the 2 species during the green forage season (Fig. 1). The only available information on cattle diets during the green forage season on annual range is the work of Wagnon (1963), who reported cattle diets for a series of dry and wet years, and for both heavy and light grazing conditions. For comparative purposes, we have extracted and graphed information from a lightly grazed pasture for a year Wagnon considered average (Wagnon 1963:12). During the green forage season, grasses were a significant part of cattle diets, ranging from a low of 10 percent in February to a high of 95 percent in July (Fig. 1A). On the other hand, grasses were only a minor part of the ground squirrel's diet. In February, filaree made up 90 percent of cattle diets, and only 20 percent of ground squirrel diets (Fig. 1B); as the season progressed, filaree became a smaller component of cattle diets, but became increasingly important to ground squirrels.

Cattle and ground squirrels showed similar seasonal patterns in their consumption of legumes and what Wagnon (1963:13) called "weeds, browse, acorns, and miscellaneous," but both classes of plants were a larger component of ground squirrel diets (Fig. 1C, 1D). Miscellaneous forbs, browse, and acorns provided only a small part of cattle diets, but they were a major part of ground squirrel diets. In February and March, when cattle were consuming small amounts of legumes, legumes were 30 percent and 40 percent, respectively, of the ground squirrel's diets. In April, when Wagnon reported cattle were consuming 50 percent legumes, ground squirrels selectively fed on them. Ground squirrels, in fact, consumed a greater part of the legume production than they did of any other plant group (Table 3). However, the maximum consumption of legumes by both cattle and ground squirrels coincided with the peak production of legumes, and it seems unlikely that the squirrels seriously limited the availability of even this minor component of the cattle diet.

In conclusion, we found that the diets of cattle and ground squirrels generally were not similar at the San Joaquin Experimental Range, the site of a number of previous studies of cattle/ground squirrel competition. We also found that ground squirrels consumed only a small amount of net above ground plant production.

### LITERATURE CITED

- BAUDINETTE, R. V. 1972. Energy metabolism and evaporative water loss in the California ground squirrel. J. Comp. Physiol. 81(1):57–72.
- CAVENDER, B. R., AND R. M. HANSEN. 1970. The microscope method used for herbivore diet estimates and botanical analysis of litter and mulch at the Pawnee Site. U.S. IBP Grassland

Biome Tech. Rept. No. 18. Colorado State Univ. 9pp.

- FITCH, H. S. 1948. Ecology of the California ground squirrel on grazing lands. Am. Midl. Nat. 39(3):513-596.
- ——, AND J. R. BENTLEY. 1949. Use of California annual-plant forage by range rodents. Ecology 30(3):306–321.
- FLATT, W. P., P. W. MOE, AND L. A. MOORE. 1969. Influence of pregnancy and ration composition on energy utilization by dairy cows. Pages 123-138 in K. L. Blaxter, J. Kielanowski, and G. Thorbek, eds. Energy metabolism of farm animals. Oriel Press, Newcastle upon Tyne, England.
- FREE, J. C., R. M. HANSEN, AND P. L. SIMS. 1970. Estimating dry weights of foodplants in feces of herbivores. J. Range Manage. 23(4):300–302.
- GOLLEY, F. G. 1961. Energy values of ecological materials. Ecology 42(3):581-584.
- GRINNELL, J., AND J. DIXON. 1918. The ground squirrels of California. Monthly Bull., Calif. State Comm. of Horticulture 7(11 & 12): 595– 807.
- HARRIS, L. D. 1971. A precis of small mammal studies and results in the grassland biome. Pages 213-240 in N. R. French, ed. Preliminary analysis of structure and function in grasslands. Colorado State Univ., Range Sci. Dept., Sci. Series 10.
- HORWITZ, W., ed. 1970. Official methods of analysis. 11th ed. Association of Official Agricultural Chemists, Washington, D.C. 1015pp.
- HOWARD, W. E., K. A. WAGNON, AND J. R. BENT-LEY. 1959. Competition between ground squirrels and cattle for range forage. J. Range Manage. 12(3):110–115.
- JOHNSON, D. R., AND K. L. GROEPPER. 1970. Bioenergetics of North Plains rodents. Am. Midl. Nat. 84(2):537–548.
- KACZMARSKI, F. 1966. Bioenergetics of pregnancy and lactation in the bank vole. Acta Theriol. 11(19):409–417.
- KLEIBER, M. 1961. The fire of life. John Wiley and Sons, N.Y. 454pp.
- MIGULA, P. 1969. Bioenergetics of pregnancy and lactation in the European common vole. Acta Theriol. 14(13):167–179.
- MORRISON, R. K. 1956. Feeds and feeding. Morrison Publ. Co., Ithaca, N.Y. 1165pp.
- SOHOLT, L. F. 1973. Consumption of primary production by a population of kangaroo rats (*Dipodomys merriami*) in the Mojave Desert. Ecol. Monogr. 43(3):347–376.
- SPARKS, D. R., AND J. C. MALECHEK. 1968. Estimating percentage dry weights in diets using a microscope technique. J. Range Manage. 21(4):264-265.
- STEEL, R. G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., N.Y. 481pp.

- TALBOT, M. W., AND H. H. BISWELL. 1942. The forage crop and its management. Pages 13–49 in C. B. Hutchison, and E. I. Kotok, eds. The San Joaquin Experimental Range. Univ. Calif., Agric. Exp. Stn. Bull. 663.
- TOMICH, P. Q. 1962. The annual cycle of the California ground squirrel *Citellus beecheyi*. Univ. Calif. Pub. Zool. 65(3):213–282.

WAGNON, K. A. 1963. Behavior of beef cows on a

California range. Univ. Calif., Agric. Exp. Stn. Bull. 799. 58pp.

- YOUSEF, M. K., W. D. ROBERTSON, D. B. DILL, AND H. D. JOHNSON. 1973. Energetic cost of running in the antelope ground squirrel, Ammospermophilus leucurus. Physiol. Zool. 46(2):139– 147.
- Received 14 December 1976.
- Accepted 4 November 1977.