ENERGY METABOLISM, NITROGEN BALANCE, AND BODY COMPOSITION OF THE FOX SQUIRREL (SCIURUS NIGER)

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ABSTRACT

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By

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Six male and six female adult fox squirrels (Sciurus niger) were livetrapped and held captive for 8 weeks, during which the daily ad libitum food intake of a commercial food (4.0415 kcal/g) was determined to be 43 g. Following that adjustment period, three specimens were randomly chosen and sacrificed for initial carcass analysis.

In a feeding experiment, the remaining nine specimens were fed for seven days at three levels of nutrition (33, 67, and 100 percent of ad libitum) to determine the maintenance energy requirements and the effect of nutritional level on metabolizable and net energy values, and on nitrogen balance. The average metabolizable energy value for all planes of nutrition for adult fox squirrels was determined to be 3.210 kcal/g, while the nitrogen-corrected metabolizable energy (ME_n) was calculated to be 2.880 kcal/g. About 79.9 percent of ingested gross energy was metabolized.

Net energy values varied considerably among levels of feed intake and previously-described methods of calculation. The maintenance energy requirement for adult fox squirrels was found to be 162 kcal/g per day per $W_{kg}^{0.75}$ of metabolizable energy or approximately 49 g per day per $W_{kg}^{0.75}$ of the experimental diet.

All feeding levels indicated a relatively high degree of nitrogen retention, which was possible as a result of high dietary levels of protein. A negative nitrogen balance was exhibited only at the 33 percent level of nutrition.

The energy content, and the percentages of moisture, protein, fat and ash were determined for the carcass of each animal. Various expected correlations were revealed when these data were subjected to regression analysis.

It seems possible that the condition of a squirrel population can be ascertained through a simple moisture analysis of captured animals which, with the established data, would enable estimations of squirrel fat and energy content. A fox squirrel population in which the adult segment exhibits a mean body energy of 5.5 kcal/g indicates one in good health, while a determination of approximately 5.0 kcal/g probably represents one in danger of immediate debilitation, death and decline.

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INTRODUCTION

In recent years, bioenergetics has become an important aspect of wildlife management. Since Lindeman (1942) formulated his concept of trophic dynamics, ecologists have become increasingly interested in the energy relationships of ecosystems. However, understanding of the energy dynamics of populations has been hampered by a general lack of knowledge concerning the energy content of many plants and animals, and the metabolism of energy and nutrients by these organisms. The fox squirrel (*Sciurus niger*) is such an organism.

The food habits of tree squirrels have been investigated by many workers (Baumgras, 1944; Barber, 1954; Nichols, 1958; Dudderar, 1967), and the effects of food on squirrel activity, behavior and reproductive success has also been examined (Seton, 1928; Allen, 1943; Uhlig, 1956; Brown and Yeager, 1945; Nixon et al., 1968). Most recent research (Smith and Follmer, 1972) has listed the food preferences of tree squirrels, and has measured the metabolizable energy of their natural foods. In another study, Ludwick et al. (1968) investigated the energy metabolism of the gray squirrel (*Sciurus carolinensis*).

To date, there has been no attempt to assess the energy and nutrient metabolism of the fox squirrel. The present study attempts to correct this deficiency of knowledge and to study the related parameters of nitrogen balance and body composition. Undertaken from October 1973 to June 1974, the specific objectives were to:

1. Assess the energy requirements of adult fox squirrels, and to study the effect of planes of nutrition on the efficiency of energy utilization.

2. Measure the nitrogen balance of adult fox squirrels under variations in both caloric and protein intake.

3. Determine the energy content, and the percentage fat, protein, moisture and ash of the body composition for specimens at various levels of nutrition.

METHODS

Fox squirrels were livetrapped under permit from two woodlots on the farm property of Michigan State University in Ingham County, Michigan. These woodlots were beech-maple stands nearly equal both in size and species composition. Hudson Woodlot was an 18-acre all-aged forest while Toumey Woodlot was a 20-acre old-growth forest stand. Both woodlots contained unhunted populations of wild fox squirrels.

Squirrels were livetrapped from late October until the last week of November, 1973. They were then held through a December and January (8 weeks) adjustment period to permit them to become accustomed to confinement and commercial food before beginning the nutritional "experimental period". Approximately 30 percent of the squirrels died in the first week of captivity, apparently the result of confinement shock (Guthrie et al., 1967). Some of the animals were revived from deep coma by subcutaneously injecting 5 ml. of a 50 percent dextrose solution and providing external heat, using a 200-watt light bulb placed near the specimen. After treatment these recovered animals were released back into their natural environment.

Sex and age was determined for each animal by the procedures outlined by Taber (1963). Twelve adult squirrels, six of each sex, were retained for study in captivity.

The feeding trials were conducted with the squirrels individually housed in 40 x 40 x 60 cm galvanized steel cages equipped with watering and feeding devices. The animals thus were allowed only a minimum of activity. Fox squirrel energy requirements measured in this investigation, therefore, were assumed to represent minimum values.

Cages were contained in an indoor animal room, completely separated from external influences. Both temperature and relative humidity were recorded both throughout the preliminary confinement period and during the later feeding trial. They were found to be relatively constant at $20.57 \pm .04°C$ and 32.5 percent, respectively. Thus, temperature stress did not contribute to the energy requirements of the captive animals.

Alternating periods of 9-hours light and 15-hours dark were maintained throughout the adjustment and experimental periods. Lake fall photoperiodicity conditions were simulated except that no changes in period-length were attempted.

During the December 20, 1973 to January 20, 1974 adjustment period, a commercial laboratory rat chow (Wayne Lab-blox) was offered ad libitum to the captive squirrels. The guaranteed analysis of this readily-accepted food was a minimum of 24 percent crude protein, 4 percent crude fat, and a maximum of 4.5 percent crude fiber.

At daily intervals throughout the feeding trials, samples of food were taken for subsequent energy determinations. The samples were ground in a Wiley mill fitted with a 9.3 mesh-to-the-sqcm screen and then pelletized with a hydraulic press. From ignitions of the pelletized samples in a Parr adiabatic oxygen bomb calorimeter (Parr Instrument Company, 1948), the average gross energy value of the food was determined to be 4.0415 kcal/g.

Water was supplied ad libitum during the adjustment and experimental periods. The squirrels were fed daily at 3:00 P.M. during both periods of confinement.

During the adjustment period, food consumption was recorded as the difference between the amount offered and that refused. The mean food consumption for all specimens during the last 13 days of the adjustment period was taken as the quantity of food eaten ad libitum during the subsequent experimental period.

Prior to the experimental period, each of the twelve squirrels was weighed to the nearest 0.1 g and placed into three groups of four animals each according to relative weight: heavy, medium, and light. One randomly-selected squirrel from each of the three groups was sacrificed for carcass analysis and determination of initial carcass energy. At this time the three remaining squirrels in each group were randomly assigned to a food intake level established at 33, 67, or 100 percent of the previously-determined ad libitum rate.

Feeding at these various levels began on January 20, 1974 at the normal feeding time. The first collection of excreta was not made until 24 hours after the first feeding of the experimental period to allow the contents of the intestinal tract to adjust to the new level of food intake.

Urine and feces were collected in 45 x 70 cm pans constructed of stainless steel. Excreta from each animal were collected at four hour intervals and, for each of the last six days of the experimental period, frozen in airtight polyethylene bags.

The experimental period was terminated at 3:00 P.M. on the seventh day. At this time the remaining squirrels were sacrificed and weighed to the nearest 0.1 g. The contents of the gastrointestinal tracts were removed, weighed and discarded. The entire carcasses were then individually ground in a Hobart grinder four times with a .95 cm hole-size plate and then three times with a .32 cm hole-size plate. Duplicate samples were removed from each of the ground carcasses and weighed with an analytical balance. The samples were then dried in a vacuum oven at 90°C for 24 hours and reweighed after cooling to room temperature in a desiccator. Weight losses were reported as moisture.

Dried samples were transferred immediately to airtight "whirl-pak" polyethylene bags to prevent absorption of atmospheric moisture. Later, these samples were ground to a semi-powder, using progressively finer meshes in a Wiley mill, and immediately returned to airtight bags. This procedure ensured near perfect homogeneity of the carcass samples. From these finely-ground samples, subsamples were extracted for analysis of energy, fat, protein, and ash.

All energy determinations were made using a Parr adiabatic oxygen bomb calorimeter. Dried subsamples of carcass about 1 g in weight were pelletized with a hydraulic press, weighed with an analytical balance, and subsequently burned. Corrections were made for oxidation of the fuse wire and acid formation.

In biological materials, the nitrogen contained in protein gives rise to nitric acid in an exothermic reaction when a sample is oxidized in a bomb calorimeter (Brent, 1974). This adds calories to determinations, therefore, the bomb was washed after each determination with an indicator solution, and the acid formed was then titrated with a standard alkali. Under these conditions, the formation of nitric acid released 13.8 kcal for each mole of acid produced. Consequently, each ml. of the 0.0725 N alkali used in the titrations was equivalent to one gram-calorie. The number of calories of heat thus produced was subtracted from the original determinations.

The percentage of protein in the carcasses was determined using the Kjeldahl semi-micro nitrogen analysis method (A.O.A.C., 1970).

A sample size of approximately 300 milligrams of dried carcass was selected for this purpose.

The Kjedahl technique involves the following three basic steps: 1) digestion of the sample in sulfuric acid, during which all organic compounds are broken down and organic nitrogen is converted to ammonium salts; 2) alkalization of the solution, distillation, and quantitative capture of the ammonia evolved; and 3) quantitation of the evolved ammonia.

There is a direct mole-per-mole relationship between ammonia released and nitrogen originally present, therefore, the volume of standard acid in ml. multiplied by the acid normality equals the milliequivalents of nitrogen in the sample. Multiplication of the number of milliequivalents by 14 (the milliequivalent weight of nitrogen) gives the total milligrams of nitrogen present. Division by the sample weight and multiplication by 100 yields percent nitrogen. Since most protein is 16 percent nitrogen, multiplication by the factor 6.25 gives percent protein.

Samples of the carcasses were analyzed for fat utilizing an ether extract procedure (A.O.A.C., 1970). Fat content was first measured as "percentage dry-matter" and then calculated as "percentage fresh-matter".

The fat-extracted samples were later placed in a muffle furnace for 20 hours at 650°C to determine ash content.

Excreta were kept frozen in polyethylene bags during the experimental period, after which they were weighed to the nearest 0.01 g. The excreta were then homogenized in a Waring blender. Subsamples were weighed to the nearest 0.01 g and placed in tared aluminum cups.

These subsamples were frozen and subsequently freeze-dried in a shelf freeze-drier.

The freeze-dried samples were then reweighed and individually ground with a mortar and pestle until homogeneous. Ground excreta samples were stored in "whirl-pak" airtight polyethylene bags for later energy and nitrogen determinations.

Excreta and food samples were analyzed for energy and nitrogen using the procedures previously outlined. These data were used to ascertain the energy balances and nitrogen balances of each specimen.

RESULTS AND DISCUSSION

Energy Balance

The average daily ad libitum food intake per specimen was found to be 43.0 g air-dry weight of the pelletized food. Since the gross energy of the food was determined to be 4.0415 kcal/g, the average total gross energy input per day ad libitum was 173.78 kcal (Table 1) for the twelve study specimens during the adjustment period.

Food intake data were collected during mid-January. These measured values of ad libitum food consumption correspond closely to the fall values reported for fox squirrels undergoing lipogenesis (Short and Duke, 1971). The observed food intake was approximately 46 percent higher than those levels previously established for January.

The high level of food consumption maintained throughout captivity indicates an environmental stimulus controlling the complex behavioral reactions of these tree squirrels. All specimens were livetrapped in October and November, and thereafter subjected to a fall light regime. Thus, it is possible that the observed variation in food consumption was a correlate of photoperiod.

The temperature and humidity were held nearly constant for the duration of confinement at $20.57 \pm .04$°C and 32.5 percent, respectively. Hafez (1967) suggested that such environmental stimuli yield a high comfort index which may result in increased food consumption and growth.

The only specimens which exhibited weight gains were those in the 100 percent ad libitum group (Table 1). The remaining specimens in the 67 percent and the 33 percent feeding levels lost an average 10 percent and 25 percent of their initial weights, respectively. None

Table 1. Energy balance over a 7-day period for 3 groups of three adult fox squirrels fed at different levels of nutrition utilizing a commercial feed with a gross energy (GE) of 4.0415 kcal/g.

Item	33%	67%	100%
Dry weight of food consumed			
Per day (g)	14.20	28.80	43.00
Per day per $W_{kg}^{0.75}$ (g/kg)	17.95	33.68	53.88
Energy intake per day (kcal, GE)	57.39	116.40	173.78
Carcass energy/animal			
Initial (kcal, GE)	4628.62	4743.31	4099.52
End (kcal, GE)	3329.74	4532.04	4232.61
Gain per day (kcal, GE)	-185.55	-30.18	19.01
Gain per day per $W_{kg}^{0.75}$ (kcal GE/kg)	-234.58	-35.29	23.82
Excreta (kcal/day)	13.14	22.65	33.62
Metabolizable energy			
Per day (kcal, GE)	44.25	93.75	140.16
Per day per $W_{kg}^{0.75}$ (kcal GE/kg)	55.94	109.65	175.64
Heat Production (H)			
Per day (kcal)	229.80	123.93	121.15
Per day per $W_{kg}^{0.75}$ (kcal/kg)	290.52	144.95	151.82

of the specimens expired from the low caloric intakes during the 7-day experimental period.

The mean value of excreta gross energy for each feeding level was determined on a daily basis (Table 1). The daily gross energy content of excreta for the 100, 67, and 33 percent ad libitum groups were 3.17, 3.29, and 3.58 kilocalories per gram dry weight, respectively.

Metabolizable energy was determined by subtracting the excreta gross energy losses from the total gross energy intake per day (Table 1). Heat production (H) (Table 1) was calculated by subtracting the average weight gain from the metabolizable energy for each group. The average heat production per day for the 6-day period was highest at the 33 percent level of feed intake (Fig. 1). This was probably due to an observed increase in activity of the squirrels of this group in their efforts to get food (Ludwick et al., 1968).

The maintenance requirements (ME_m) for adult fox squirrels were determined by a method similar to the one described by Lofgreen (1965). These calculations indicate that the energy equilibrium in adult fox squirrels could be maintained with a daily dietary level of 162 kcal of metabolizable energy per $W_{kg}^{0.75}$ (Fig. 2). Ludwick et al. (1968) indicated that adult gray squirrels (_Sciurus carolinensis_) required 167 kcal of metabolizable energy per $W_{kg}^{0.75}$ per day to maintain energy equilibrium. Therefore, the maintenance requirements of the two species are almost identical.

Approximately 49 g per day per $W_{kg}^{0.75}$ of the experimental diet would supply the amount of metabolizable energy required for maintenance by adult fox squirrels (Fig. 3). This is also comparable to the value of 56 g per day per $W_{kg}^{0.75}$ determined for adult gray squirrels in

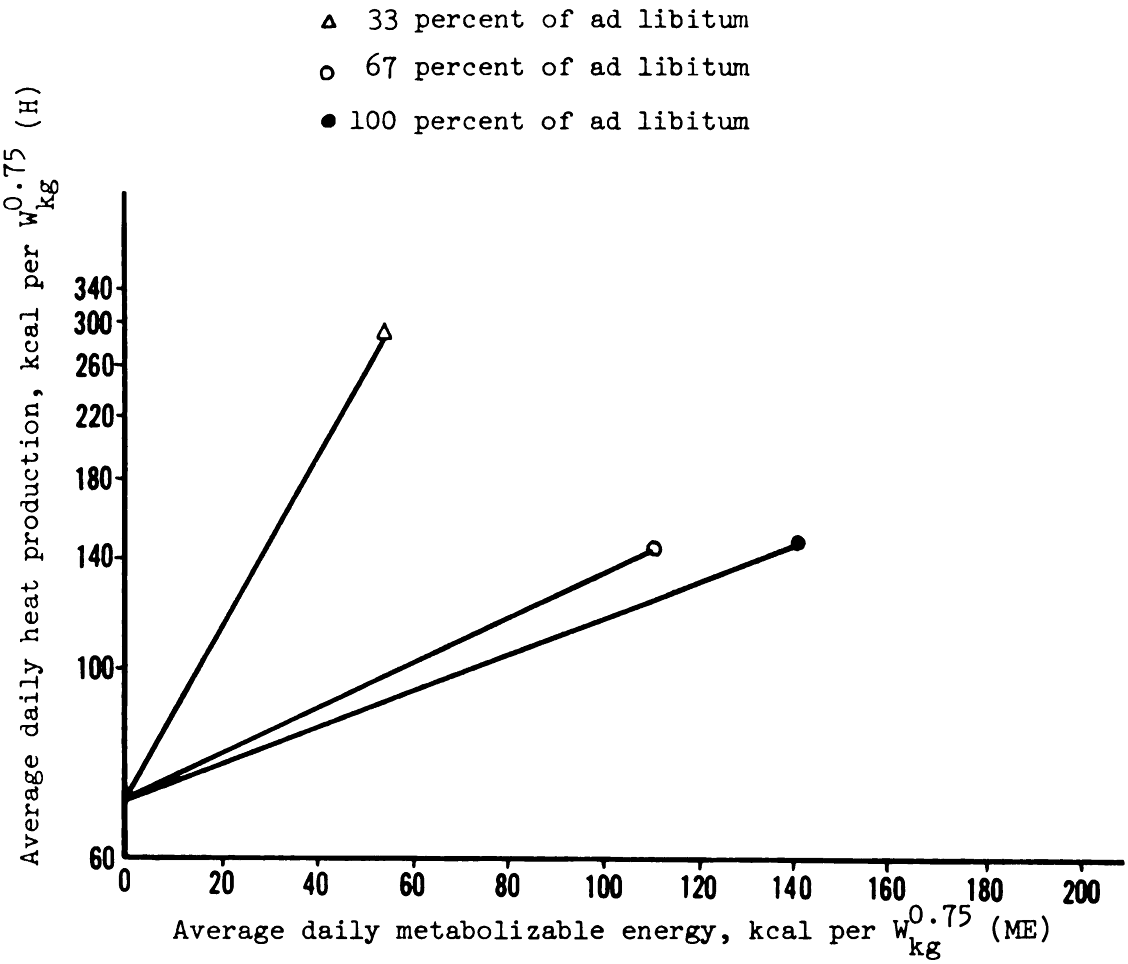

Figure 1. The relationship between heat production and metabolizable energy for 3 groups of three adult fox squirrels fed at different levels of nutrition for 7 days.

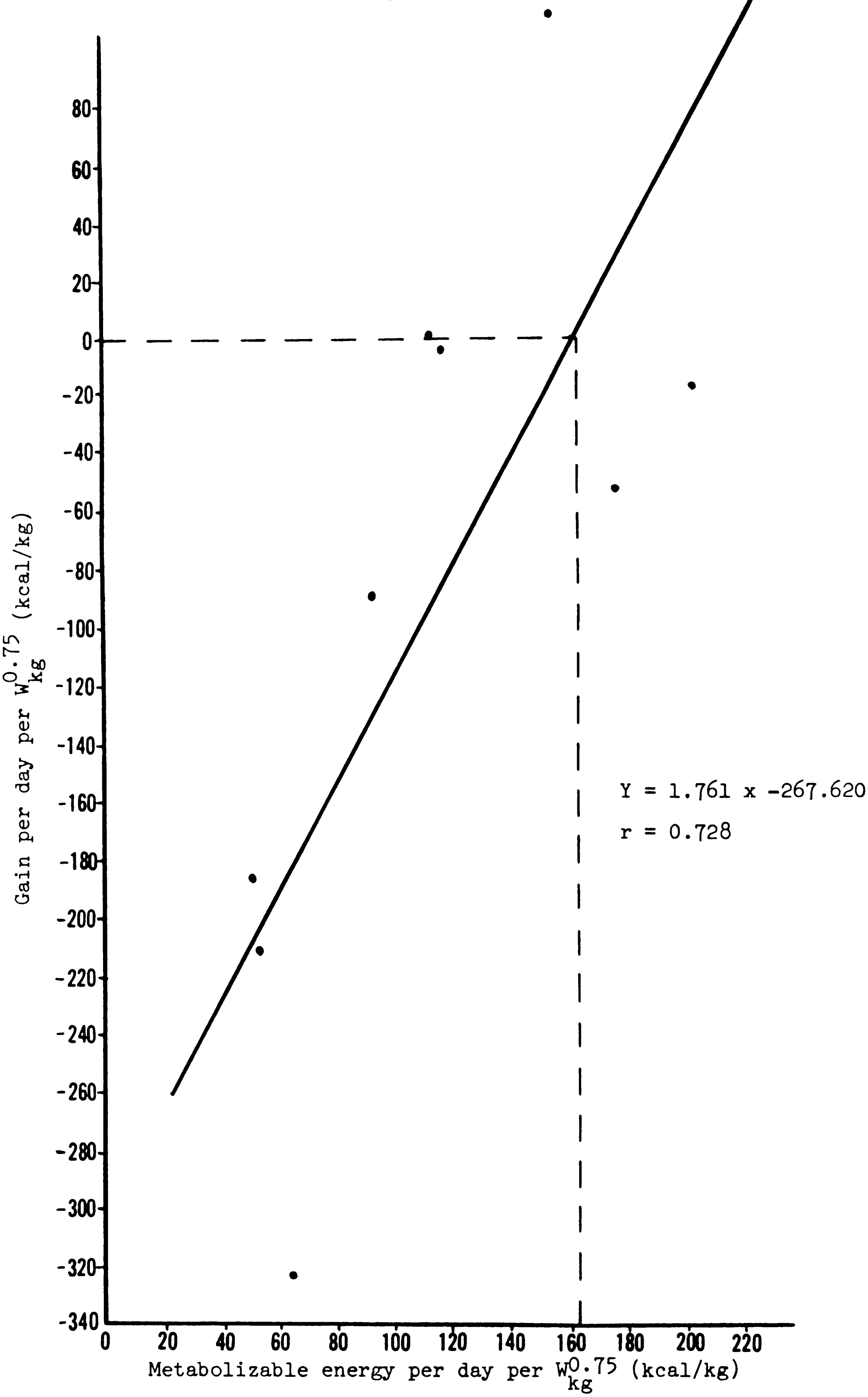

Figure 2. Metabolizable energy required for the maintenance of adult fox squirrels, determined with a method similar to the one described by Lofgreen (1965).

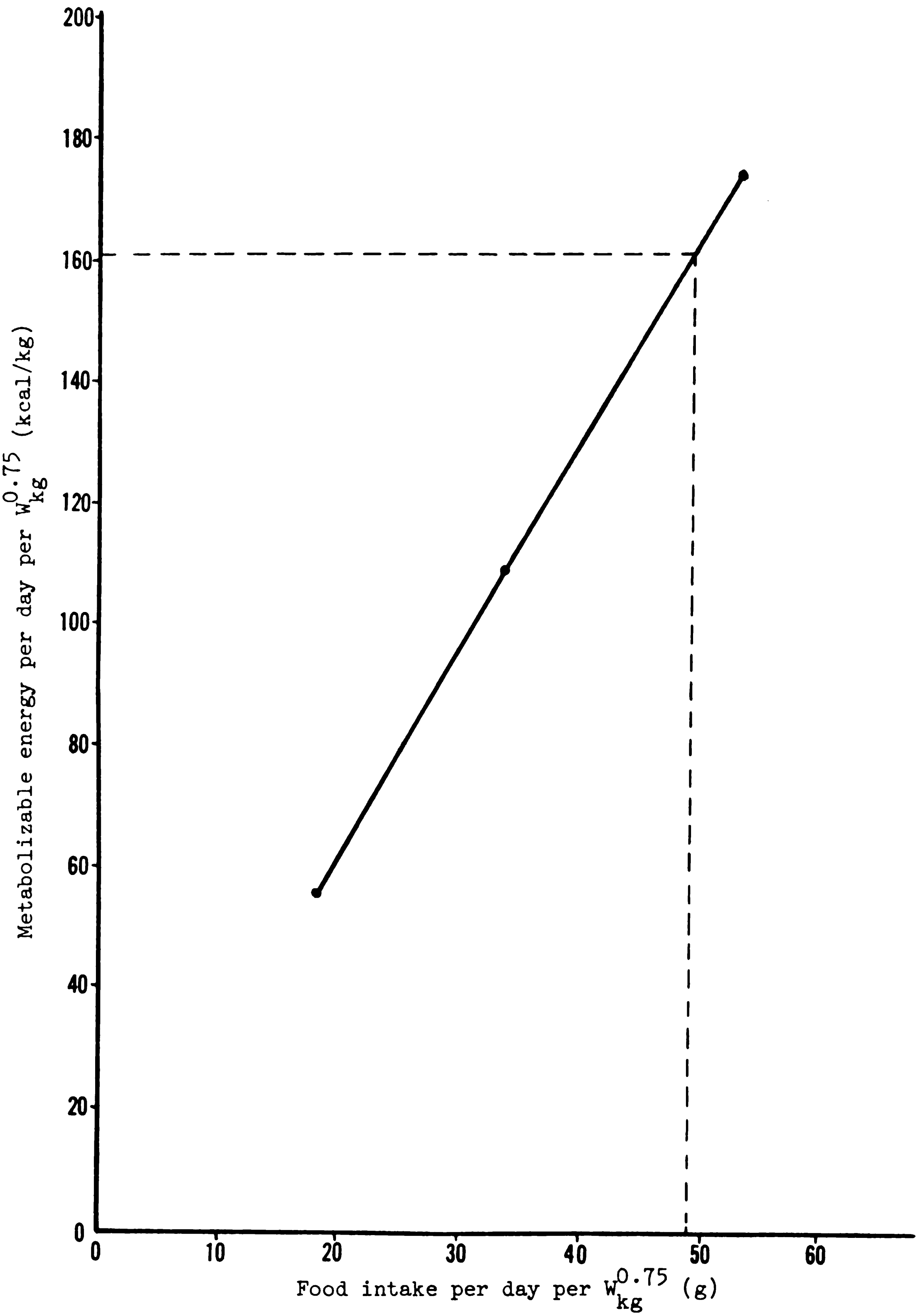

Figure 3. Quantity of food (Wayne Lab-blox) required to maintain adult fox squirrels, determined with a method described by Lofgreen (1965).

captivity (Ludwick et al., 1968). The average ad libitum food intake for the fox squirrel is approximately 30 percent over that calculated for maintenance.

It is commonly thought that, for small game animals, winter is the seasonal "bottleneck" which determines carrying capacity (Leopold, 1933). Thus, the main goals of management have been directed toward the manipulation of the winter environment to bring a maximized breeding stock through this period. The reality that winter is a critical period of the year is especially significant for fox squirrels since it is also their breeding season (Allen, 1943).

The level of carrying capacity may not be the sole result of the length or severity of the winter season in energy limited populations. In this study, animals in previously good condition were able to withstand relatively long periods of caloric restriction (7 days @ 33 percent of ad libitum food intake) under the conditions of confinement. Fox squirrels are probably physiologically capable of storing enough energy during autumn lipogenesis to help sustain themselves for the winter months. However, as is often the case, density-induced competition or mast crop failure may render sufficient energy resources unavailable for consumption and subsequent storage. The carrying capacity of an area, therefore, may be dictated by the energy available prior to the critical winter period, since a sufficient fall supply of food energy is necessary to the successful wintering and breeding of a population.

The management of fox squirrels in temperate zones, and perhaps other wildlife which undergo energy storage in preparation for the winter months, possibly should be directed more toward increasing the amount and availability of fall food stocks when the supply is insufficient or undergoes extreme yearly variation.

The mean metabolizable energy values for all three levels of food intake (Table 2) was 3.210 kcal/g, with 79.9 percent of the total energy intake metabolized. The metabolizable energy values apparently increased significantly (F test at $\alpha = .05$) with each increase in the plane of nutrition (Table 2). When the metabolizable energy was corrected to nitrogen equilibrium (N-corrected metabolizable energy or ME_n), however, the values decreased significantly (F test at $\alpha = .05$) with each increase in the plane of nutrition (Table 2). This significant decrease in ME_n with each increase in food intake indicates a higher degree of efficiency in energy utilization with increasing caloric restriction.

The necessary correction was made as follows: for each gram of nitrogen lost from the body (equal to negative nitrogen balance) 7.45 kcal were added to the metabolizable energy and for each gram of nitrogen retained in the body (equal to positive nitrogen balance) 7.45 kcal were subtracted from the metabolizable energy. The correction used (7.45) was obtained (National Academy of Sciences 1411:1966) with dogs and may not be entirely correct for other animals.

Net energy (NE) values varied considerably among the methods of calculation used, with this variation occurring both within the same and at different levels of nutrition. Net energy values calculated by both methods (Lofgreen and Otagaki, 1960; Swift, 1957) were much higher at the 67 percent ad libitum feeding level than at the 100 percent level. The total NE of the restricted diet may be expected to be somewhat higher per gram than the same diet fed at a higher level

Table 2. Metabolizable and net energy values of the experimental diet (Wayne Lab-blox) for nine adult fox squirrels fed for 7 days at three planes of nutrition.[a]

Item	Percent of Ad Libitum 33 (n=3)	67 (n=3)	100 (n=3)
Metabolizable energy (ME) (kcal/g)	3.116	3.255	3.260
N-corrected metabolizable energy (ME_n) (kcal/g)	3.304	2.926	2.409
Net energy (kcal/g)[b]	---	10.640	3.464
Net energy of feed increment (kcal/g)[c]	---	12.667	2.926

[a]Based on the data from Table 1.

[b]Refers to net energy of increment between the 67 and 100 percent levels and the 33 and 67 percent levels using Swift's (1957) method.

[c]Refers to net energy of feed increments as above using a procedure described by Lofgreen and Otagaki (1960).

of intake, since the restricted animals were closer to maintenance, and the NE of a feed is generally higher for maintenance than for production (Lofgreen and Otagaki, 1960).

These NE values are probably greatly exaggerated in the calorically restricted diets, however, since the heat increment used in the calculations is partially the result of the metabolism of body tissues and is not entirely the result of food energy metabolism. Therefore, only NE values above maintenance should probably be considered valid if calculated by either of the aforementioned methods.

Nitrogen Balance

A determination of nitrogen in the food and excreta under the previously described controlled conditions provided a quantitative measure of the protein metabolism and specifically indicated whether the specimens were gaining or losing protein. The specimens in the 33 percent level of nutrition had an average daily nitrogen intake 59.58 mg less than the total outgo from their bodies (Table 3). These animals were thus in a negative nitrogen balance. Squirrels in this group were losing 372.38 (59.58 x 6.25) mg of protein from their bodies daily, representing the amount by which the ingestion of protein fell short of meeting the needs of the animals for maintenance.

An excess of intake over outgo, representing a positive nitrogen balance and involving a storage of protein, was exhibited by both the 67 and the 100 percent groups (Table 3). These groups showed average daily positive balances of 212.19 mg and 818.69 mg, respectively. Therefore, as also found by Calloway and Spector (1955), nitrogen excretion becomes progressively greater as the energy supply is reduced.

Table 3. Nitrogen intake, excretions, and balance in 9 adult fox squirrels at three levels of caloric and protein intake during a 6-day experimental period.

Feeding level (% ad libitum)	Animal Number	Nitrogen (average mg/day) contained in: Food	Excreta	Nitrogen Balance
	6	1355.36	336.76	1018.6
100	8	1355.36	552.23	803.13
	10	1355.36	721.03	634.33
	2	908.35	653.47	254.88
67	3	908.35	842.61	65.74
	7	908.35	592.41	315.94
	1	447.87	622.65	-174.78
33	4	447.87	674.76	-226.89
	9	447.87	224.93	222.94

The positive nitrogen balance indicated in the 67 percent feeding level was surprising at first, since restriction of caloric intake usually results in a catabolism of protein for energy. Numerous investigations (Allison et al., 1946; Stevenson et al., 1946; Benditt et al., 1948; Rosenthal, 1952) have shown, however, that nitrogen utilization is a function of not only caloric intake but also of protein intake.

It was demonstrated by Allison et al. (1946) that nitrogen balance in the dog was unaltered provided 50 percent or more of the caloric requirement was met. In studies employing protein-depleted rats (Stevenson et al., 1946), supplemental egg protein or methionine was effective in sparing body protein when only 50 percent or more of the energy requirement was supplied. Rosenthal (1952) reported a positive nitrogen balance when casein (phosphoprotein of milk) protein supplementation was increased to 0.30 mg/kg body weight.

In this study the relatively high levels of nitrogen retention were probably the result of a high dietary level of protein (approximately 20 percent). As in the aforementioned studies, this level of dietary protein intake probably supplied sufficient nitrogen to achieve positive balance, even in the calorically-restricted 67 percent level of nutrition.

Carcass Energy and Body Composition

Although the thermodynamic approach to ecology has been applied in many instances (Lindeman, 1942; Odum and Pinkerton, 1955; Patten, 1959; Slobodkin, 1960), a full understanding of the energy dynamics of individual populations has been hampered by incomplete knowledge of the energy content of many plants and animals.

Studies concerning ecological productivity or energy flow often require the expression of biomass in total caloric values (Odum, 1971; Krebs, 1972). Biomass is usually converted to energy by using caloric equivalents obtained from the literature. Many workers are reluctant to depend on equivalents, and have made their own energy determinations for various living materials in a bomb calorimeter.

The caloric value of the tissue of small mammals has been previously determined for only eight species. Golley (1959, 1960) studied samples from 4 species of Microtus pennsylvanicus Ord and established their caloric value as equal to 4.650 kcal/g dry weight. He (Golley, 1959; in Davis and Golley, 1963) also determined the energy value for white mice (Mus musculus L.) to be 5.675 kcal/g. Golley (1961) later reported the mean for both of these species to be 5.163 kcal/g. Sharp (1962) determined the caloric value of Oryzomys palustris Harlan as equal to 5.840 kcal/g.

Gorecki (1965) examined five species of small mammals and determined their caloric values per gram dry weight. The percentages of water and ash were also determined. In the examined rodents the kcal/g dry weight value were the lowest at the end of winter at 4.508 kcal/g, while in the summer and fall the values increased rapidly to reach 5.261 kcal/g. The seasonal caloric value for the body tissue of shrews remained relatively constant year around at approximately 4.554 kcal/g. He also found that seasonal fluctuations and specific differences in these values depended mainly on the fatness and only slightly on the ash content of the animals.

In the present study, energy values per gram dry weight were determined for the carcasses of the twelve fox squirrels used in this investigation (Table 4). The 100 percent feeding level (n = 3) and the initial slaughter group (n = 3) revealed similar mean energy values of 5.554 and 5.550 kcal/g dry weight, respectively. These values, which represent animals undergoing lipogenesis in the fall, are similar to the summer and fall values for rodents examined by Gorecki (1965) and Golley (1959).

A mean energy value of 5.925 kcal/g dry weight was determined for the specimens of the 67 percent level of nutrition. This high value probably reflects the presence of large fat reserves as indicated by the somewhat higher initial weights of the animals randomly placed in this group.

The 33 percent feeding level group yielded a mean energy value of 5.256 kcal/g of carcass. This low value evidently was a result of caloric deficiency resulting in depletion of body fat reserves. An individual which was near death in this group exhibited a body energy content of only 4.861 kcal/g.

From the specimens observed in this study, a reduction in body energy to a value near 5.0 kcal/g dry weight reflects a very poor condition and a squirrel which is near death.

In addition to energy composition, percentage moisture, protein, fat and ash were also determined for the carcasses of each animal (Table 4). When subjected to regression analysis, these data revealed an inverse linear relationship (r = -0.96) between energy (kcal/g dry matter) and percentage moisture (Fig. 4). A similar relationship has been established also for domestic livestock (Maynard and Loosli, 1959). A direct linear relationship (r = 0.99) was found (Fig. 5) between energy (kcal/g dry matter) and percentage fat of dry matter

Table 4. Percentage composition and energy content of the carcasses of twelve adult fox squirrels.

Feeding Level	Animal Number	Moisture	Fat		Protein		Ash		Energy (kcal/g)	
			Dry Matter	Fresh Matter	Dry Matter	Fresh Matter	Dry Matter	Fresh Matter	Dry Matter	Fresh Matter
Initial slaughter group	5	66.01	17.44	5.93	65.19	22.16	12.07	4.10	5.284	1.796
	11	63.82	23.73	8.58	63.39	22.93	13.04	4.72	5.811	2.102
	12	65.17	19.75	5.46	66.48	23.50	11.11	3.87	5.555	1.935
100 percent of ad libitum	6	58.26	36.55	15.26	50.61	21.12	8.69	3.63	6.368	2.658
	8	67.75	14.23	4.59	74.28	23.95	12.18	3.93	5.261	1.697
	10	69.49	8.48	2.58	74.54	22.74	12.47	3.80	5.034	1.536
67 percent of ad libitum	2	51.86	28.39	13.67	47.23	22.74	21.61	10.40	5.313	2.557
	3	57.86	36.19	15.25	49.31	20.78	10.24	4.32	6.186	2.607
	7	59.13	36.92	15.09	48.79	19.94	8.78	3.59	6.276	2.565
33 percent of ad libitum	1	63.34	23.51	8.62	61.90	22.69	10.62	3.89	5.659	2.075
	4	68.09	7.28	2.32	75.57	24.11	15.32	4.89	4.861	1.551
	9	69.11	11.39	3.52	71.76	22.17	10.30	3.18	5.249	1.621

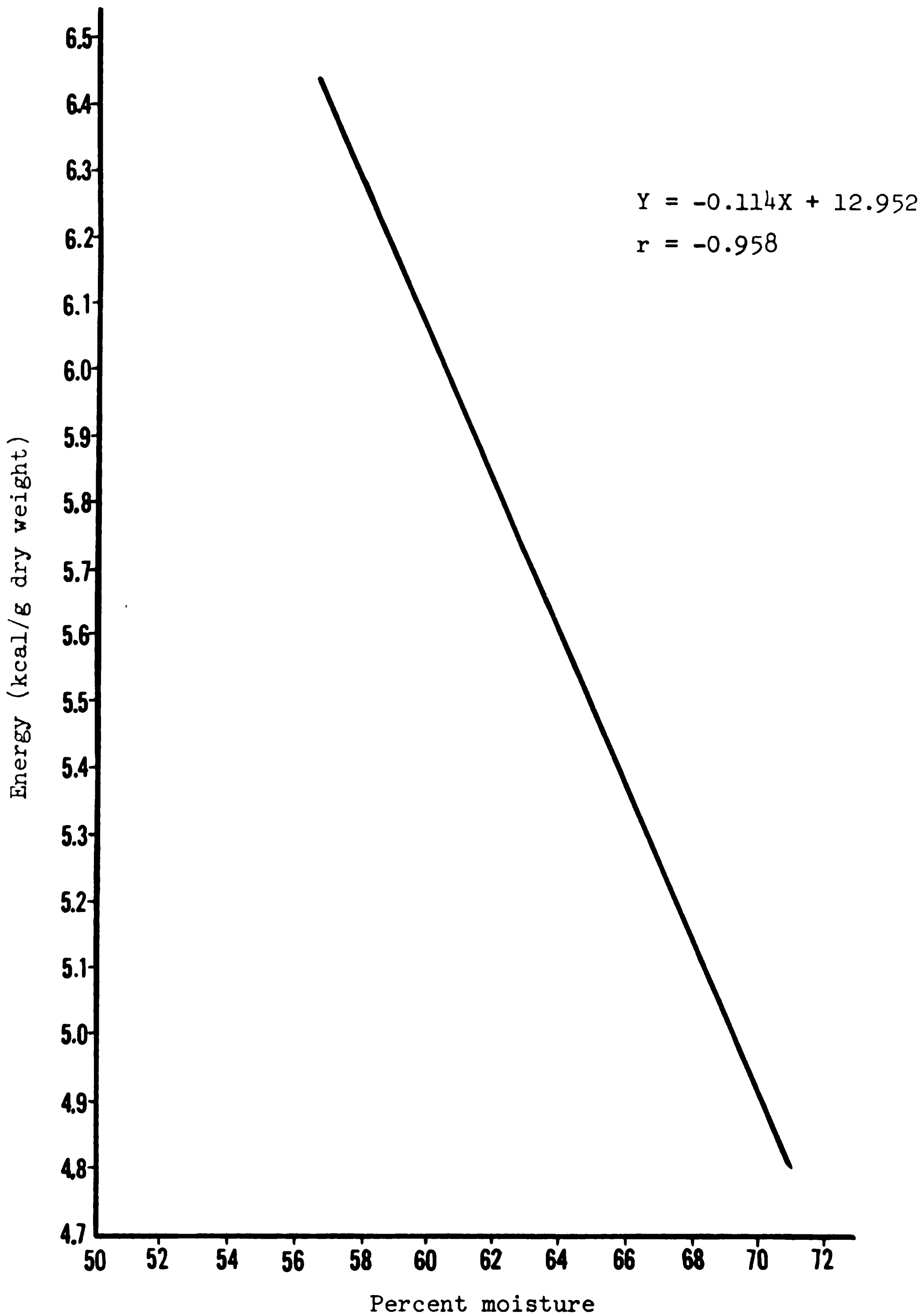

Figure 4. The relationship between energy (kcal/g dry weight) and percentage moisture for the carcasses of twelve adult fox squirrels.

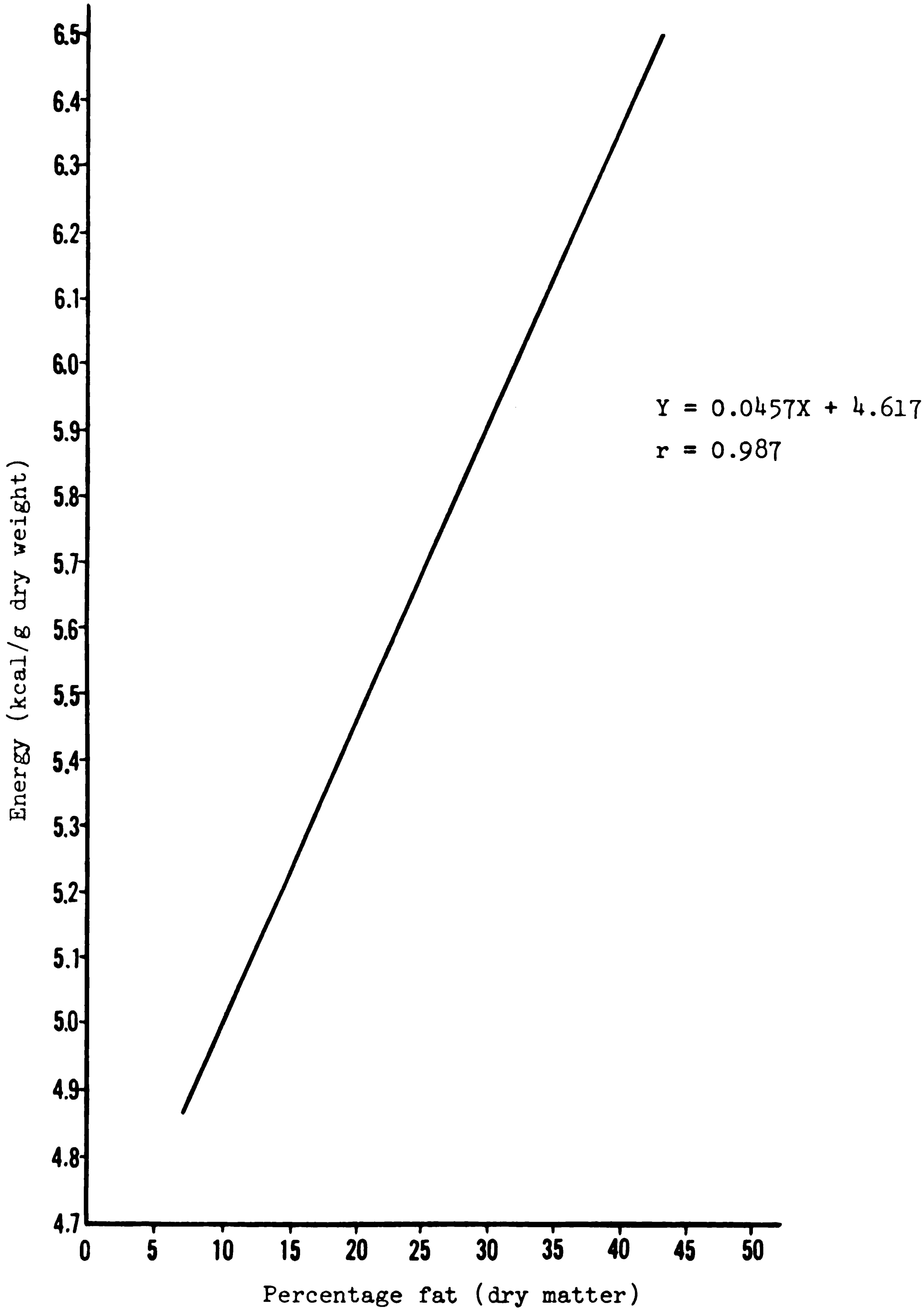

Figure 5. The relationship between energy (kcal/g dry weight) and percentage fat (dry matter) for the carcasses of twelve adult fox squirrels.

and a similar relationship (r = 0.97) between energy (kcal/g dry matter) and percentage fat of fresh matter (Fig. 6). These relationships are probably the direct result of the high energy content of fat tissues (9.45 kcal/g dry matter) (National Academy of Sciences 1966:1411).

Although the percentage protein in fresh matter remained relatively constant with a mean of 22.40$\pm$.36 (s.e.), the percentage protein of dry matter indicated an inverse linear relationship (r = -0.96) with energy (kcal/g dry matter) (Fig. 7). This indicates that the percentage protein in the fresh carcass remains relatively constant, while fat and moisture fluctuate inversely with each other (Fig. 8). Therefore, when the fat content is high protein makes up only a small percentage of the dry matter (Fig. 9). The inverse was also indicated by the data. Hence, a direct linear relationship (r = 0.98) between percentage moisture and percentage protein of dry matter was revealed (Fig. 10). The percentage ash of the total fresh weight remained nearly constant at about 4 percent.

The knowledge of either carcass energy, percentage protein (dry weight), percentage fat (fresh or dry weight), or percentage moisture allows the remaining parameters to be rather accurately estimated utilizing the linear regression correlations presented in the data (Fig. 4-10). These data may serve as a means to ascertain the condition of adult squirrel populations at various times of the year. Slobodkin (1961) indicated that cal/g energy values may provide an index of the nutritional condition of animals in the field which would be considerably cheaper and as reliable as the elaborate sampling programs now required.

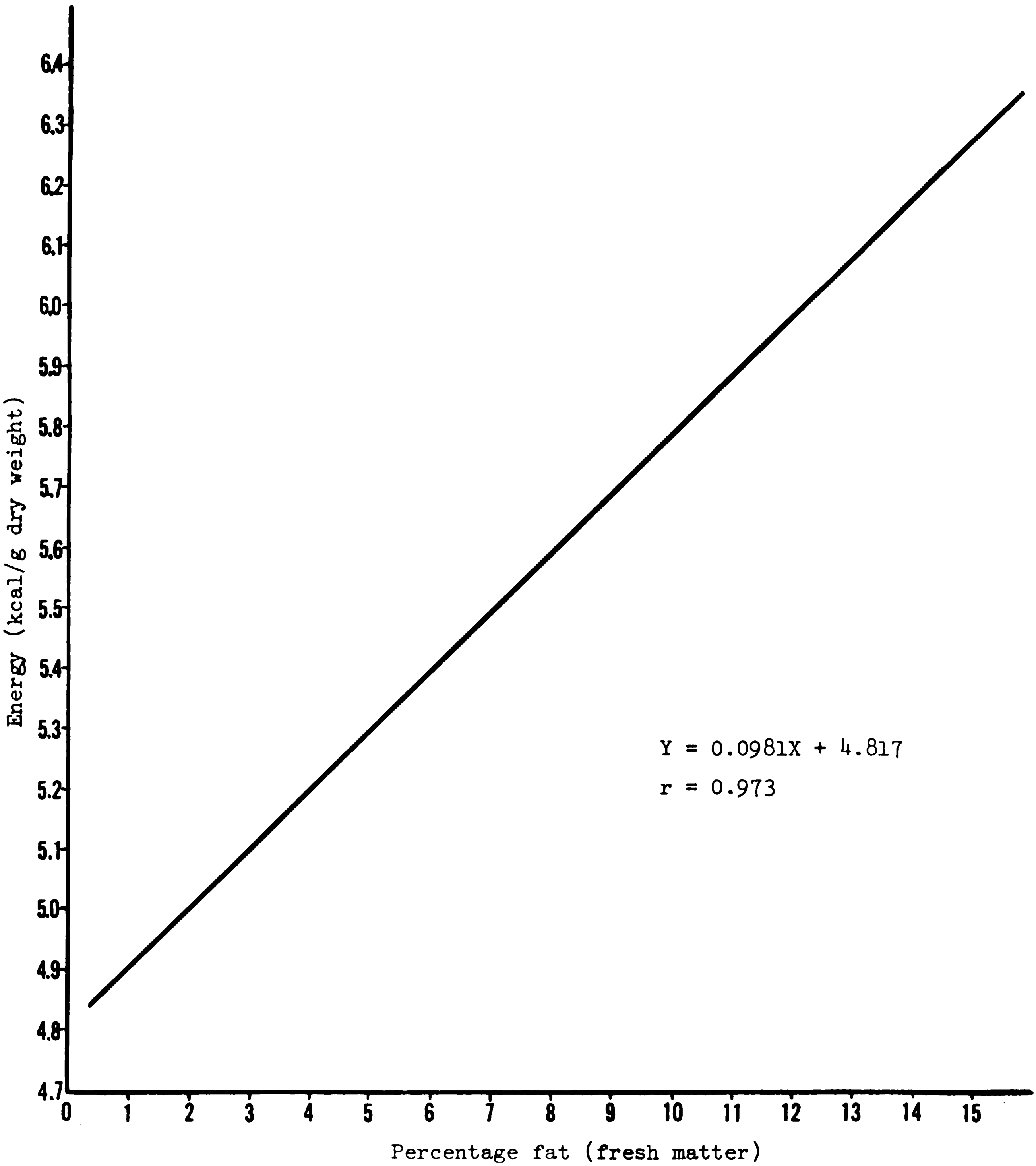

Figure 6. The relationship between energy content (kcal/g dry weight) and percentage fat (fresh matter) for the carcasses of twelve adult fox squirrels.

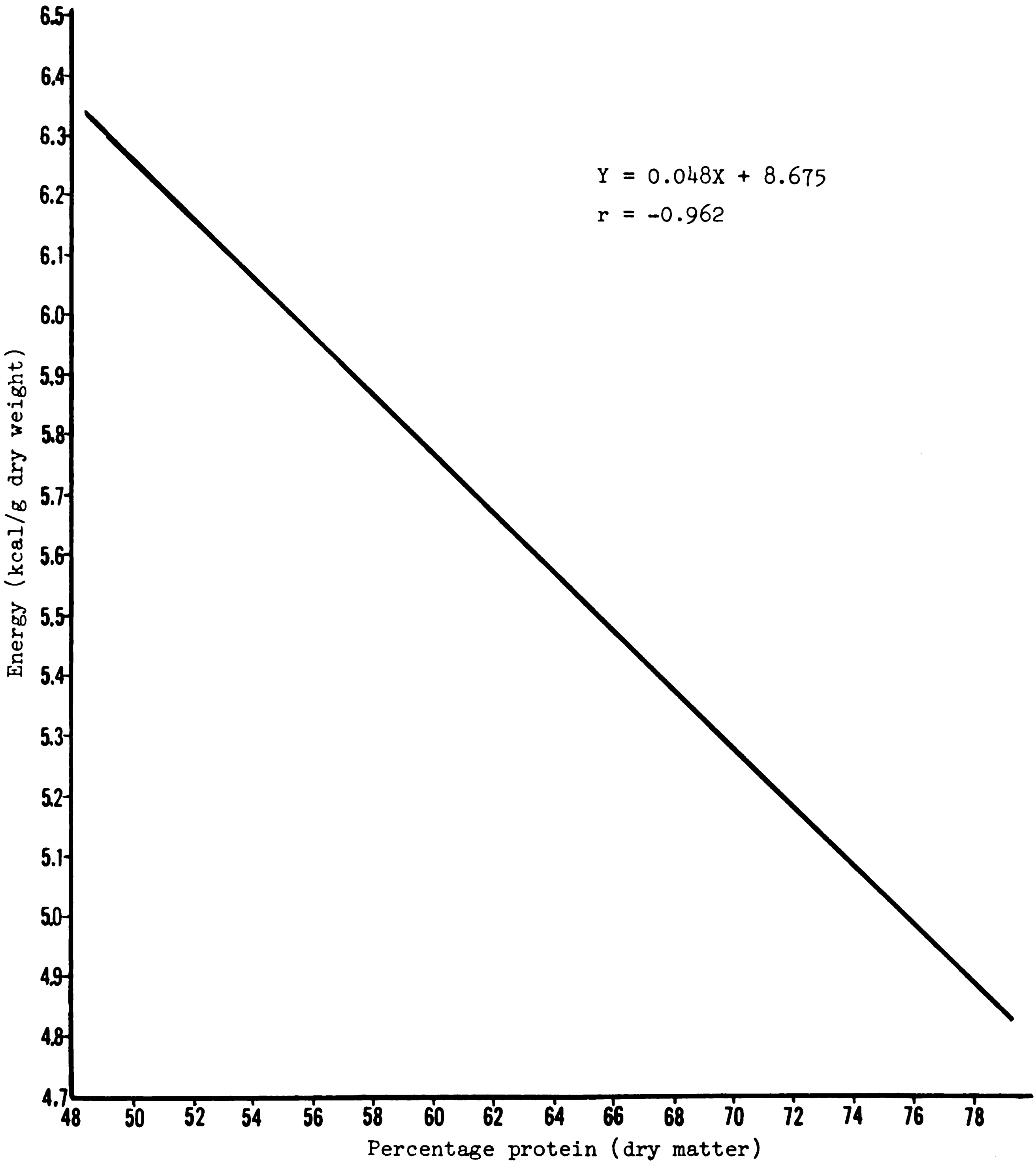

Figure 7. The relationship between energy content (kcal/g dry weight) and percentage protein (dry matter) for the carcasses of twelve adult fox squirrels.

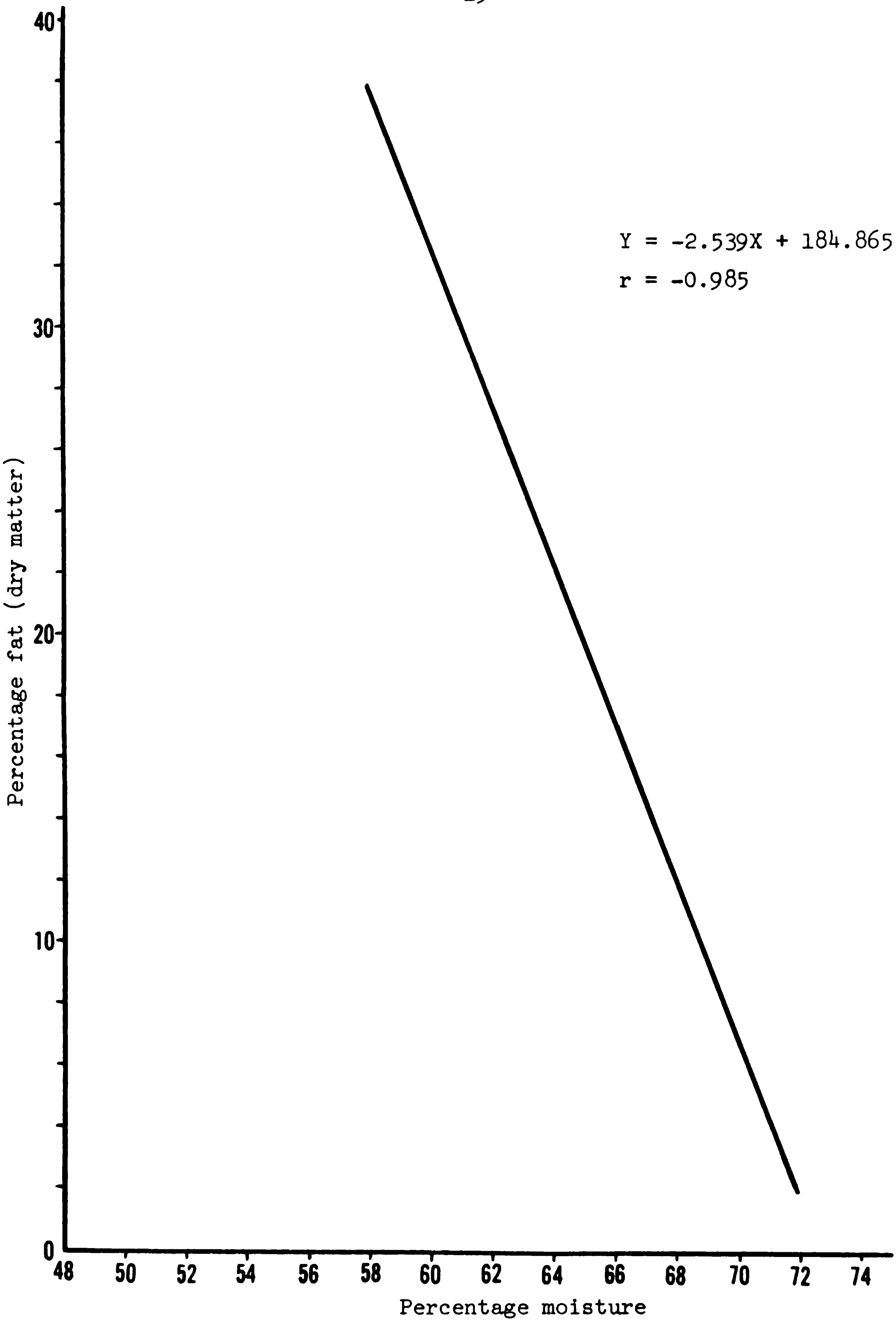

Figure 8. The relationship between percentage fat (dry matter) and percentage moisture for the carcasses of twelve adult fox squirrels.

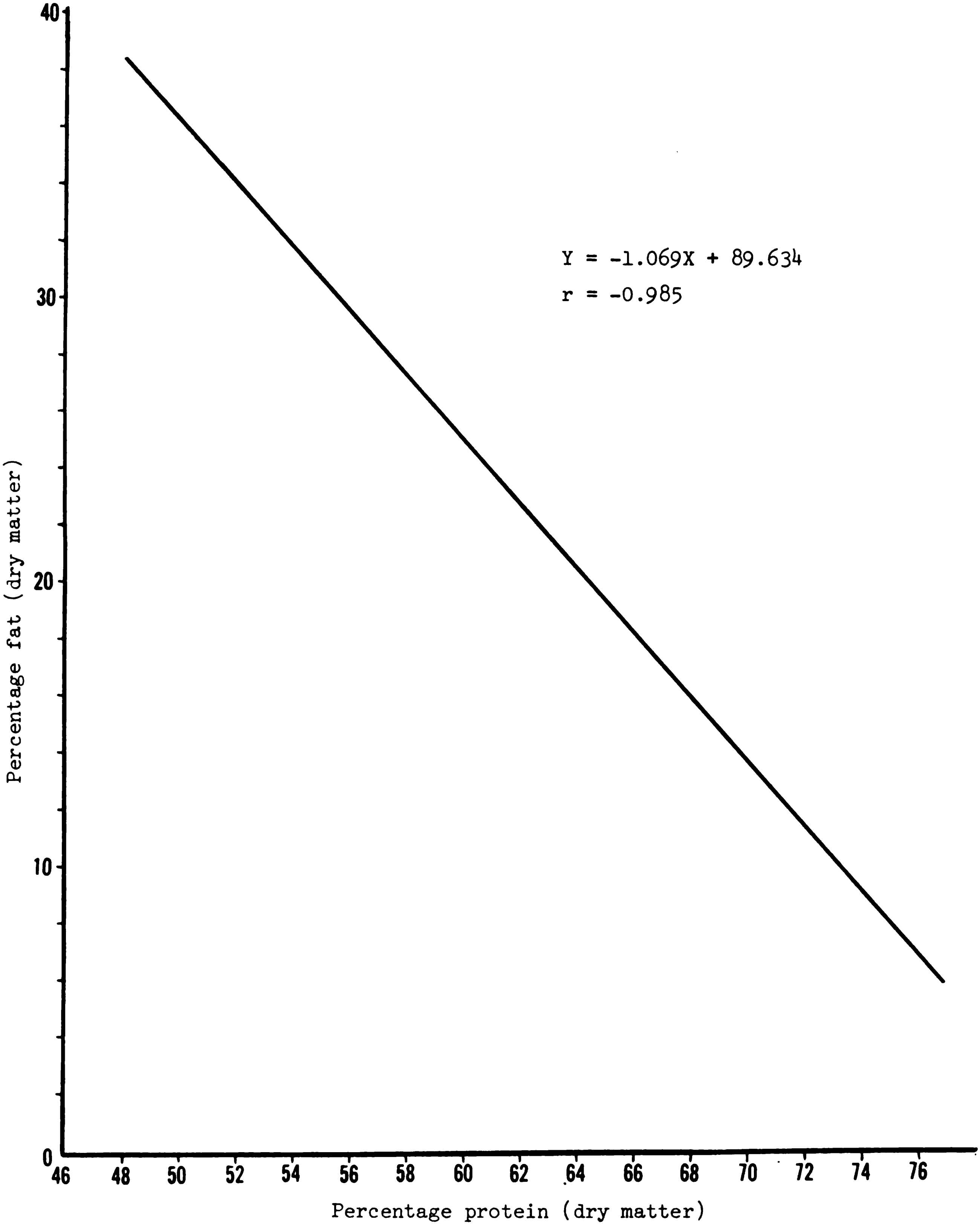

Figure 9. The relationship between percentage fat (dry matter) and percentage protein (dry matter) for the carcasses of twelve adult fox squirrels.

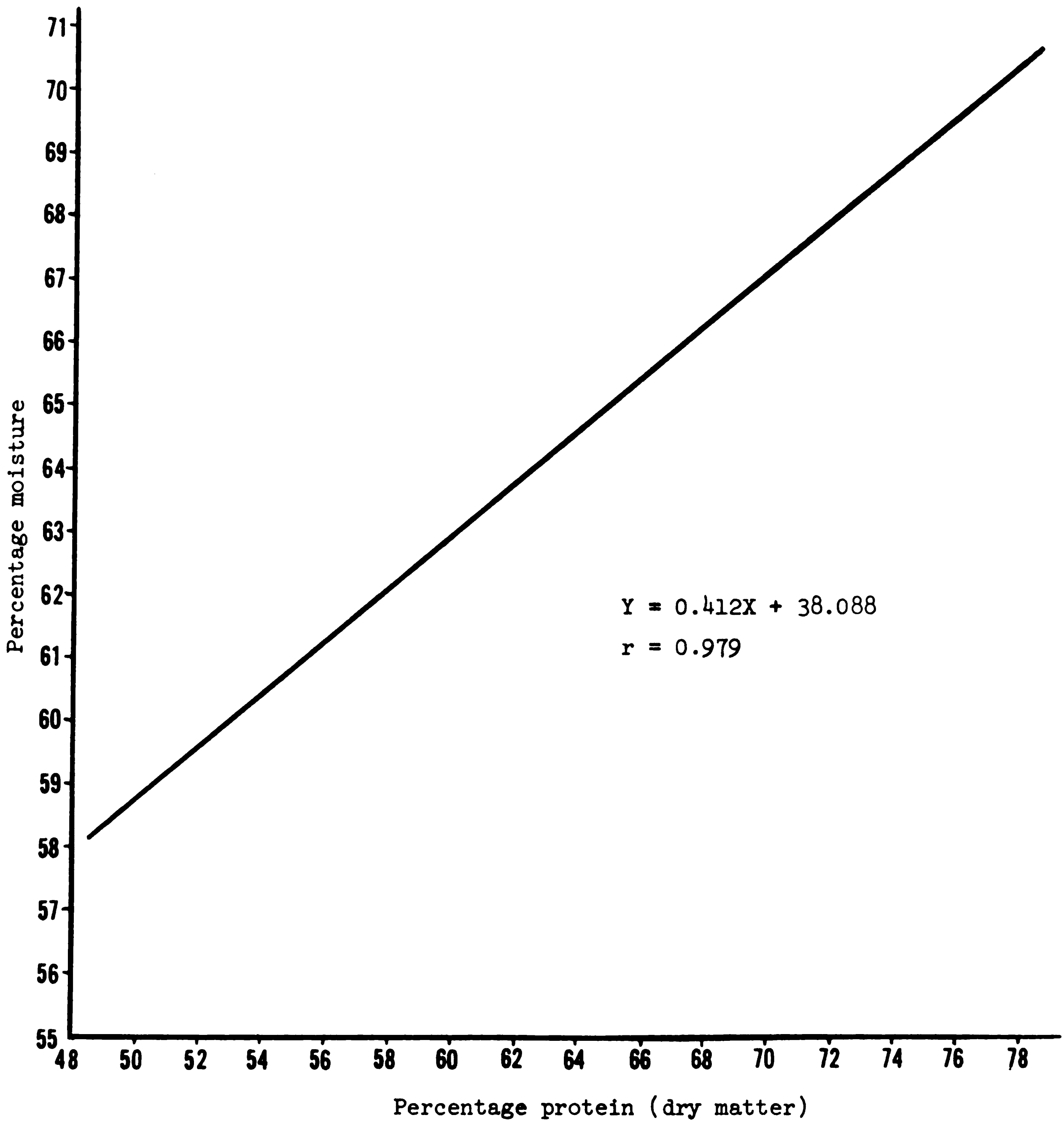

Figure 10. The relationship between percentage moisture and percentage protein (dry matter) for the carcasses of twelve adult fox squirrels.

A relatively small adult segment of a fox squirrel population could be randomly removed and simply analyzed for moisture with the use of only a vacuum oven and a balance. Using the regression formulae presented in the data, the moisture analysis would in turn yield percentage fat content and energy (kcal/g) of the carcasses. These calculated data would serve as an index of the population's condition.

Mean energy values of 5.0 kcal/g dry weight would probably indicate an adult population which has undergone a negative energy balance and is in very poor condition.

Future research might be directed toward a correlation between percentage moisture or fat and specific gravity. Specific gravity could be measured with a gas-displacement apparatus without sacrificing specimens. Such a correlation would, with the use of the previously established regression formulae, give quantitive values of body composition and condition for adult fox squirrels.

SUMMARY

A study was undertaken during 1973-74 to determine various parameters concerning the energy metabolism, nitrogen balance, and nutritive body composition of the fox squirrel (Sciurus niger). Six male and six female adult fox squirrels were livetrapped from two similar woodlots on the farm property of Michigan State University. During an 8 week adjustment period in captivity, the average daily ad libitum food intake of a commercial food (Wayne Lab-blox, 4.0415 kcal GE/g) was 43 g.

Although the experimental and adjustment periods were in mid-January, the ad libitum level of food intake corresponded to previously established fall values (Short and Duke, 1971). The observed high ingestion of food was probably the result of the fall light regime imposed upon the animals throughout their confinement.

Following the adjustment period, three specimens were randomly chosen and sacrificed for initial carcass analysis. The remaining specimens were divided equally (reps) and fed at three levels of nutrition (33, 67, and 100 percent of ad libitum) for seven days. During this experimental period, urine and feces were collected and frozen in airtight bags for later energy and nitrogen analyses.

Data collected during the experimental period were used to determine the maintenance energy requirements and the effect of nutritional level on the metabolizable and net energy values, and on the nitrogen balance. The average metabolizable energy value for all planes of nutrition for adult fox squirrels was 3.210 kcal/g, while the N-corrected metabolizable energy (ME_n) was calculated to be 2.880 kcal/g.

The N-corrected metabolizable energy increased with increased caloric restriction, indicating a progressively higher efficiency of utilization at the lower planes of nutrition.

An average of about 79.9 percent of ingested gross energy was metabolized. Net energy values varied considerably among levels of feed intake and methods of calculation. The maintenance energy requirement for adult fox squirrels under these prescribed conditions was calculated to be 162 kcal/g per day per $W_{kg}^{0.75}$ of metabolizable energy or approximately 49 g per day per $W_{kg}^{0.75}$ of the experimental diet. The average daily ad libitum food intake in calories (173.78 kcal GE) exceeded the maintenance requirements by about 30 percent.

A determination of the nitrogen content in food and excreta provided a quantitative measure of protein metabolism and indicated whether the specimens were gaining or losing protein. Nitrogen excretion became progressively greater as the energy intake was reduced. A negative nitrogen balance was exhibited at the 33 percent level of nutrition. All feeding levels indicated a relatively high degree of nitrogen retention, which was possible as a result of high dietary levels of protein. This level of protein intake probably supplied sufficient nitrogen to achieve a positive balance, even in the calorically-restricted 67 percent level of nutrition.

The energy content, and the percentage moisture, protein, fat and ash were determined for the carcass of each animal. Various correlations were revealed when these data were subjected to regression analysis. It seems likely that the condition of a fox squirrel population can be ascertained through a simple moisture analysis of captured animals which, with the established data, enable estimations of squirrel body fat and energy content.

An adult fox squirrel population with a mean body energy of 5.5 kcal/g indicates one in good health while a determination of approximately 5.0 kcal/g probably represents one in danger of immediate debilitation, death and decline.

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