ENERGY DYNAMICS OF A FOOD CHAIN OF THE OLD-FIELD COMMUNITY

By

Frank Benjamin Golley

AN ABSTRACT

Submitted to the School for Advanced Graduate Studies of Michigan State University of Agriculture and Applied Science in partial fulfillment of the requirements for the degree of

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Frank Benjamin Golley

ABSTRACT

The vegetation - Microtus pennsylvanicus pennsylvanicus Ord - Mustela rixosa allegheniensis Rhoads food chain of the perennial grass-herb stage of old-field succession was studied from May, 1956 to September, 1957. Primary objectives of the study were to determine 1. the rate of synthesis of organic matter by the vegetation, 2. the path of energy from the vegetation, through the mice, to the weasel, and 3. the losses of energy at each step in the food chain.

The total solar insolation during the 1956 growing season at East Lansing was 94.2×10^8 Calories per hectare. Primary net production of the vegetation was separated into three components: 1. production of above-ground vegetation, 2. production of roots, and 3. plant production consumed by Microtus. From these data it was estimated that net production totaled 49.51×10^6 Calories per hectare in 1956 and 44.25 Calories per hectare in 1957. Respiration of the vegetation, examined by crude field calorimetery, appears to approximate 15 per cent of the total assimilation. By calculation from the two preceding estimates gross primary production ranged from 58.27×10^6 Calories per hectare in 1956 to 53.01×10^6 Calories per hectare in 1957.

Tissue production, mortality, and production of young of Microtus were studied in the field by live-trapping. Metabolic rate and food consumption were investigated in the laboratory. Food consumption of the mouse population was

estimated at 249 x 10^3 Calories per hectare per year. Of this energy consumed by the mice, 5170 Calories were utilized in tissue production and 170 x 10^3 in respiration of the mouse biomass. Food consumption and respiration estimates were based on rates established in the laboratory as .14 grams of food consumed per gram mouse tissue per day and 10 Calories used in respiration per mouse per day.

The dynamics of the weasel population was studied incidental to the Microtus program. Population densities and growth rates were estimated from limited trapping data. Net production of the weasel population was 130 Calories per hectare per year, and respiration energy loss was 5434 Calories per hectare. Food consumption, based on laboratory experiments, totaled 5824 Calories per hectare per year.

Of the solar energy available to the vegetation, 1.2 per cent was used in gross production and 1.1 per cent in net production. Of the energy available to the Microtus 1.6 per cent was consumed as food, and 1.1 per cent was used in growth and respiration. The weasel consumed 31 per cent of the net production and immigration of the Microtus population.

Twenty-one per cent of the net production of the Microtus population and 10 per cent of the weasel net production was lost from the food chain through other predators or microorganisms. Of the energy consumed only a portion was used in production of tissue; most of this energy was used in respiration, in maintaining normal activity, or passed

through the digestive tract unused. The respiration energy loss increased from the vegetation base to the weasel level of the food chain. Maintenance energy loss was not estimated. The gross energy in the food in experimental diets recovered in the feces amounted to 10 to 18 per cent in Microtus and 10 per cent in Mustela.

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INTRODUCTION

In recent years there has been a growing interest in the study of the transfer of energy through natural systems (ecosystems, Tansley, 1935). Park (1946) stated that, "probably the most important ultimate objective of ecology is an understanding of community structure and function from the viewpoint of its metabolism and energy relationships." Aquatic biologists have generally taken the initiative in the study of community energetics and most of the information available today concerns fresh water or marine communities. A great need exists for similar studies on terrestrial communities. With additional data we will be able to determine if the concepts developed for aquatic environments have equal application to terrestrial environments.

A subdivision of community energetics, the food chain, was chosen for intensive study, since the elucidation of energy transfer through a complete terrestrial community was considered impossible of fulfillment in a short time by a single investigator. The transfer of food energy from plants, through a herbivore, and one or several carnivores is called a food chain (Odum, 1953). The food chain does not exist as an independent entity; rather it is an artificial but useful concept allowing some schematization of organismal relationships within the community. Thienemann (1926)

expressed this same concept in his catagories of producers (obtaining energy for synthesis of organic matter from solar energy) and consumers (obtaining energy by feeding on producers). The food chains within the community are interrelated complexly, but organisms obtaining their food by the same number of steps can be considered members of the same trophic level (Lindeman, 1942). Food chains and trophic levels are separate concepts both of which pertain to a linear hierarchy of assimilative relationships.

In this study a food chain of the old-field community, from perennial grasses and herbs to the meadow mouse, Microtus pennsylvanicus pennsylvanicus Ord, to the least weasel, Mustela rixosa allegheniensis Rhoads, was chosen for investigation. Burt (1948) was used as the authority for all mammal nomenclature. This food chain included the dominant vertebrate of the community (Microtus) and one of its main predators (Mustela), but excluded the otherwise important insects, other invertebrates, bacteria, and fungi. The primary objectives of the study were to determine: 1. the rate of synthesis of organic matter by the primary producers (the vegetation), 2. the path of this energy from the vegetation, through the mouse, to the weasel, and 3. the losses of energy at each step in the food chain.

Description of the Area

The study area was located in a large field on the Michigan State University State Farm approximately one mile south-east of Okemos, Ingham County, Michigan (sec. 27, T. 4N, R. 1W). As far as was known, this farm was last tilled in 1918 when it was given to the State of Michigan by a Mr. John Fink. It was acquired by Michigan State University in 1940 and was pastured from 1940 to 1942. The study area has been undisturbed since 1942, with the exception of some tree planting by the Department of Forestry, Michigan State University, and probably occasional burning. The tree plantings appeared to be only slightly successful. The vegetation on the area was unburned from January, 1952 to March, 1957.

The field in which the study area was located was situated on the north terrace of the Red Cedar River, approximately 20 feet above the level of the river. The topography was gently undulating, with a relief not exceeding 15 feet (Figure 1). A shallow depression ran through the center of one of the trapping areas and served as a drain during heavy rains in the winter and spring. On February 9, 1957 the snow melt-water was approximately seven inches deep in this drainage area. As the snow melted in February and March much of the study area was inundated, with grass hummocks and the hills providing the only dry sites.

The soils on the study area were predominantly Conover

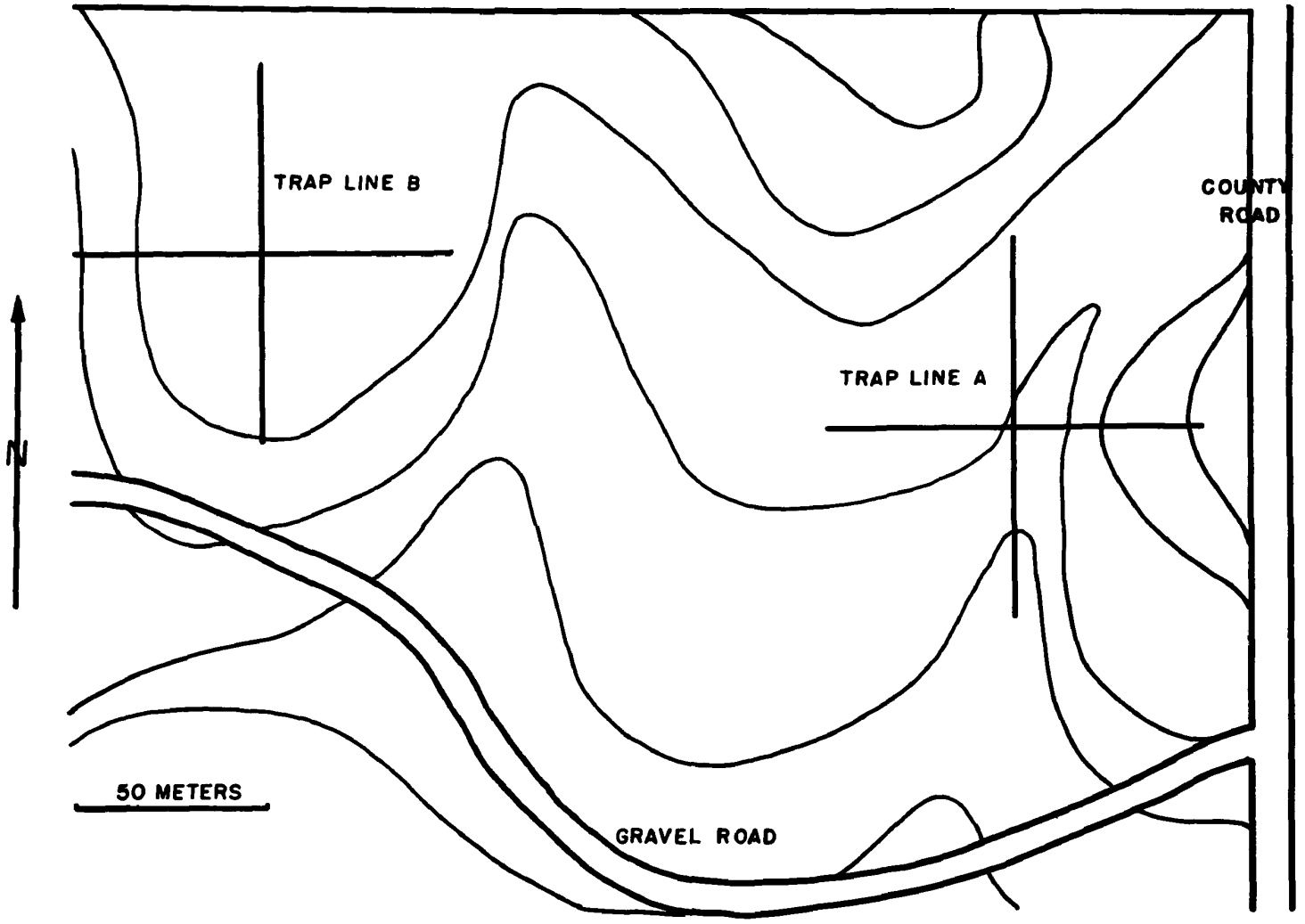

Fig. 1 - Generalized topographic map, drawn from field observations, showing location of two trap areas. Contour interval is 2.5 feet. Highest contours in the north.

and Miami loam (determined from the soil map by Veatch et al., 1941).

On the east the field was separated from similar habitat by a macadam county road. The north boundary was predominantly pasture land or orchard. The west boundary was an experimental alfalfa field which was left uncut in 1957. To the south the field was bounded by an unused gravel road, which ran along the ridge top above the river terrace and separated the field from other old-field vegetation containing more woody cover and indicating a latter stage of old-field development. The field itself contained approximately 10 hectares of contiguous habitat.

The climate in this area of Michigan is characterized by cold winters and mild summers. Yearly percipitation at East Lansing (1911 to 1949) averages 31 inches; growing season percipitation averages 17 inches. The mean annual temperature is approximately 47°F, with extremes ranging from -20° to +102°F. The growing season (last day in spring and the first day in fall when the temperature reaches 32°F) averages 147 days. This summary of weather patterns was compiled from Baten and Eichmeier (1951). Solar radiation at East Lansing (three miles west of the study area) is peculiar in that a plateau in the insolation curve may be expected about April 25 to May 20. When solar energy received at East Lansing is compared with that for most of the 92 weather stations in North America measuring solar insolation, it is evident that East Lansing

receives annually less solar heat than any other station with the exception of Fairbanks, Alaska (Crabb, 1950b).

No attempt was made to make a complete survey of the flora and fauna of the community preparatory to the study. During the investigation a list of the most abundant plants and vertebrate animals was compiled incidental to other work. Table 1 shows the frequency (per cent of total plots) with which plant species were encountered in the study quadrats (one-quarter square meter). The vegetation of the study area, see Figures 2, 3, and 4, was transitional between the perennial grass stage (perennial grasses predominate) and the perennial herb stage (perennial herbs codominate with the grasses) of old-field succession (Beckwith, 1954). The vegetation could also be considered similar to the bluegrass-upland association of Blair (1948) and the upland community of Evans and Cain (1952).

Canada blue grass, Poa compressa[1], was dominant over the entire area, with three herb species, Daucus Carota, Cirsium arvense, and Linaria vulgaris, sharing dominance in portions of the area. The study area could be divided into four facies on the basis of codominance of the above herbs with Poa compressa. Mosses, undeveloped small herbs, and grass shoots formed a subordinate layer beneath the grass and perennial herb layer. A woody overstory occurred sporadically over the area, consisting primarily of Crategus spp., Pyrus communis, and Prunus pennsylvanica.

[1] Authorities for vascular plant binomials are the same as in Fernald (1950).

TABLE 1

FREQUENCY WITH WHICH PLANT SPECIES WERE ENCOUNTERED ON 145 STUDY QUADRATS (¼ m^2)

Species	Frequency (Per Cent)	Species	Frequency (Per Cent)
Poa compressa[1]	100	Rumex Acetosella	4
Daucus Carota	63	Hypericum punctatum	4
Taraxacum officinale	37	Verbascum Thapsus	2
Cirsium arvense	26	Asclepias verticillata	2
Linaria vulgaris	22	Hedeoma pulegioides	2
Solidago spp.	22	Potentilla recta	2
Trifolium repens	18	Carex spp.	2
Achillea Millefolium	12	Agrostis alba	1
Plantago spp.	7	Aster spp.	1
Monarda punctata	7	Medicago sativa	1
Phleum pratense	4		

[1]Authority for taxonomy of plants Fernald (1950).

TABLE 2

THE NUMBER OF TIMES VERTEBRATE SPECIES, EXCLUDING BIRDS, WERE OBSERVED ON THE STUDY AREA FROM MAY, 1956 TO OCT.,1957

Species	Number of Observations	Type of Observation
Microtus pennsylvanicus[1]	546	trap
Blarina brevicauda	95	trap
Peromyscus maniculatus	25	trap
Mustela rixosa	15	trap
Zapus hudsonicus	13	trap
Sylvilagus floridanus	7	sight
Thamnophis sirtalis	5	sight
Rana palustris	3	sight
Rana pipiens	3	sight
Storeria dekayi	2	sight
Canis familiaris	2	tracks
Citellus tridecemlineatus	2	trap
Sorex cinereus	1	trap
Mephitis mephitis	1	sight
Felis domesticus	1	sight
Tamiasciurus hudsonicus	1	trap
Mus musculus	1	trap

[1]Authority for taxonomy of mammals Burt (1948), of reptiles Pope (1947).

Fig. 2 - Northwest view of the study area, August, 1956. Note discontinuous woody overstory. Daucus Carota in bloom.

Fig. 3 - North view of the study area, November, 1956. One trap line is shown in the center of the photograph. A heavy stand of dead grass and herbs appears in foreground.

Fig. 4 - West view of the study area, November, 1956. The second trap line is shown to the right of the center of the photograph. Flowerstalks of Daucus Carota in the foreground, with a stand of Poa compressa in the depression in the center of the photograph.

The woody plants were a relatively unimportant component of the vegetation, the percentage cover for all woody plants averaging approximately 0.5.

The vertebrate dominants of the community were Microtus pennsylvanicus and Blarina brevicauda, when total number observed was used as the criterion of dominance. Other vertebrate associates, based on trapping records, sight observations, and tracking observations are recorded in Table 2.

Survey of the Literature

The study of the energy dynamics of the community received great impetus in the United States after Lindeman (1942) formulated his trophic-dynamic aspect of ecology. Lindeman, in collaboration with Hutchinson and drawing on the work of Juday (1940) and others, developed and clarified a number of concepts pertaining to community energetics. The present study can be considered a natural extension of the orientation of American work toward study of the trophic aspects of the community. However, it also meets Ivelev's (1945) criticism of Lindeman's trophic level concept. Ivelev suggests that trophic levels are an abstraction, since the species making up one level may often include herbivores, carnivores, and omnivores; rather the greatest concern should be for the ecosystem or the separate food chain. The reasonableness of the study of a single food chain is further indicated by Shoryfin (unpublished, quoted by

Ivelev, 1945), who found in a study of the fish in the Caspian Sea that, although a food web did exist, for each species there was little more than one dominant prey group.

As previously mentioned (p. 2), Lindeman pointed out that more or less discrete trophic levels could be recognized in the community and that these could be pictorially represented by an "Eltonian pyramid." Lindeman also showed that while the percentage of loss of energy due to respiration becomes greater at the higher trophic levels, the percentage utilization of available energy increases. Clarke (1946) clarified the concepts of (1) standing crop or the amount of organisms existing at the time of observation, (2) material removed or yield, and (3) production or the rate at which organisms are formed within an area. Odum and Pinkerton (1955) suggested that biological systems operate at the optimum efficiency for maximum production, which is always less than maximum efficiency. Odum (1956) criticizes Lindeman and Clarke for considering production synonymous with energy intake. He suggested that production be considered as the rate of synthesis of plant or animal organic matter. Ivelev (1945) made a detailed analysis of the concepts concerning the biological productivity of waters as developed by American and European ecologists.

Community energetics has been studied in the field by a number of workers, these include Borutsky (1939), in Lake Beloie; Juday (1940), in Lake Mendota, Wisconsin;

Lindeman (1941), in Cedar Bog Lake, Minnesota; Clarke (1946), at Georges Bank; Odum and Odum (1955) at Eniwetok Atoll; and Odum (1957) in Silver Springs, Florida. Fewer workers have been concerned with the dynamics of one or several separate food chains in a single community. Some direct information is available on food chains from studies of the influence of one fish species on bottom organisms (Hardy, 1925).

A voluminous literature exists concerning the energetics of organisms in one trophic level or of one species. Leibig (1840) probably made the first calculations of the magnitude of the world photosynthesis. Other workers, including Ebermayer (1885), Arrhenius (1908), Ciamacian (1913), Schroeder (1919 a and b), Noddack (1937), Riley (1944), Gaffron (1946), Steeman-Nielsen (1952), and Terrien, Truffaut and Carles (1957), surveyed the accumulating data and arrived at other estimates of the photosynthetic efficiency of the world vegetation. Riley (1944) estimates the total photosynthesis plus respiration of the world to be in the region of $14.6 \pm 8.7 \times 10^{10}$ tons of carbon per year. Brown (1905), Briggs (1929), Transeau (1926), and Rabinovitch (1945) have been concerned with the efficiency of photosynthesis of plants, ranging from that of one leaf to that of an entire stand of vegetation. The energetics of the invertebrates of a forest soil has been studied by Bornebusch (1930). Brody (1945) has summarized the large literature on the

bioenergetics of domestic and wild animals, especially as related to growth.

From study of the literature, we might expect that: 1. the efficiency of conversion of available energy to net production will increase in each successive step from producer to consumer levels of the food chain, and 2. the percentage of energy lost in the respiratory process will increase from the lowest to the highest levels of the food chain.

METHODS

Solar Insolation

Records of solar insolation (the rate at which solar energy is received on a horizontal surface at the surface of the earth) were obtained from the Michigan Hydrologic Research Station (the Agricultural Research Service, USDA, and the Michigan Agricultural Experiment Station cooperating). The Station operates an Eppley ten-junction thermopile, thermoelectric pyrheliometer, mounted atop a small instrument house located on an isolated section of the Michigan State University Farm, East Lansing. There is little smoke contamination at this location (Crabb, 1950a) and it was assumed that the records obtained at the pyrheliometer were applicable to the study area approximately three miles to the east.

Vegetation

The vegetation was studied from August, 1956 to September, 1957. Midway through the investigation (March, 1957) a fire destroyed the vegetation on one-half of the study area, and it was necessary to move the entire operation to another portion of the same field. Fortunately there were few differences in vegetation, topography, and soils evident at these two locations.

Square clip-plots (one-quarter square-meter in size) were used to estimate the standing crop of vegetation. All plant stems within the quadrats were clipped at the ground level. The cut vegetation was transferred to

plastic bags and transported to the laboratory, where live grasses, live herbs, and dead vegetative materials were separated according to species. These materials were then dried at 100°C for 24 hours and weighed. Monthly data were averaged and standing crop of vegetation was expressed in grams of dry weight per one-quarter square meter. Ten to twenty random clip plots were chosen for investigation each collection period, with the exception of late March. The adverse weather conditions in the latter part of March allowed an estimate to be made of green vegetation on only two plots.

Samples of several months collections of dried grasses and herbs were randomly chosen for calorific analyses. These materials were ground in a Wiley Mill. Three subsamples from each species sample were analysed in a Parr adiabatic bomb calorimeter.

The standing crop of roots and above-ground portions of the plants which escaped clipping were also determined at three periods during the 1957 growing season. At each collection, five of the ten to twenty plots which had been clipped just prior to the root sampling were chosen at random and a piece of sod, 225 square-centimeters in area, was cut from each plot. The sod was later washed in running water, oven dried at 100°C and weighed to determine average weight of roots per square meter. The samples were taken to a depth of 15 cm. and could not be considered to represent the complete root biomass.

Shively and Weaver (1939) show that the roots of many prairie plants extend at least several feet into the soil. For this study it was assumed that the main mass of roots in the old-field community were concentrated within 15 cm. of the surface.

The standing crop of vegetation measured here, is less than the total amount of organic matter synthesized over the growing season (net production, Odum, 1956). This is because the standing crop includes neither the amount of vegetation which grew and died between the periods of measurement, not the amount of vegetation consumed by animals. In this study, some dead vegetation of the current growing season was included with the green vegetation since no effort was made to separate the dead and living portions of one leaf or small plant. The material that grew and died back to the ground during the current growing season was included with the dead vegetation and would be a source of error in determination of net production. The magnitude of this error was not estimated.

The amount of vegetation consumed by Microtus was inferred from feeding experiments and stomach sample analyses. The food consumption of herbivorous insects and other invertebrates, which in the pasture community may be of considerable magnitude (Wolcott, 1937), was undetermined.

Another source of error in estimating the net production of the vegetation is that pointed out by

Pearsall and Gorham (1956). They suggest that in perennial vegetation the peak standing crop is formed from (1) the accumulation of the organic matter during the present season and from (2) that stored in the roots the previous season. The techniques used in this study allowed no estimate of the contribution of the previous seasons production to the current peak standing crop.

To obtain a complete estimate of the energy utilization of vegetation (gross production, Odum, 1956) the energy used in respiration of the vegetation must be added to the net production. A field calorimeter was devised to make a rough measure of the respiration of the vegetation and the soil organisms. Two five-quart oil cans were forced five centimeters into the ground at randomly chosen sites on the study area. Gases were withdrawn from the cans into Bailey gas analysis bottles. Carbon dioxide and oxygen content of the air in the cans was determined in an Orsat-Henderson gas analysis apparatus. Cans were placed in the ground and the first samples were withdrawn approximately one hour after dark. The second sample was taken in the early morning when the air temperature at the ground surface was approximately equal to the air temperature observed when the first samples were withdrawn the previous night. The consumption of oxygen and production of carbon dioxide over the night (12 hours) was determined as the differences in the percentage composition of oxygen and carbon dioxide in the air in the cans at the first and

second sampling. No measurement was made of the diffusion of gases between the soil and the air under the cans. The RQ (CO_2/O_2) was calculated and the thermal equivalent (in Calories) of the oxygen used and the carbon dioxide produced was extrapolated from the tables in Brody (1945). Respiration was then expressed as Calories used per gram of plant tissue per hour respiration during the night.

The Microtus Population

The energy dynamics of the Microtus population were studied both in the field and by laboratory experiments. In the field a live-trapping program was initiated in May, 1956 and continued to September, 1957. This program was designed to yield information on population density, mortality, growth rate, and production of young. The trapping design was suggested by Hayne (unpublished) and consisted of two crossed trap lines, 100 meters long, with the live traps spaced two meters apart. One trap line was operated for 24 hours, it was then unset and the line crossing it was set for 24 hours. The total trapping period extended for 6 days, with 3 days for each line. Since by the sixth day of trapping unmarked animals were generally caught only in the end traps in a line, it was assumed that six days of trapping was adequate to capture most of the animals living in the trap area. Twenty-five per cent of the captures of unmarked animals occurred on the last two days of trapping (Table 3). However, if the unmarked animals captured in the last 10 traps at each

TABLE 3

EFFECT OF EXCLUDING NEW CAPTURES IN THE END TRAPS ON PERCENTAGE OF NEW CAPTURES DURING THE LAST TWO DAYS OF TRAPPING, BOTH LINES OF TRAPS

Period	Total New Captures	All New Captures Last Two Days		New Last Two Days, For Center 30 Traps	
	Number	Number	Per Cent of Total	Number	Per Cent of Total
May	8	0	00	0	00
July	19	5	26	3	16
Sept.	17	3	18	0	00
Oct.	16	4	25	1	06
Nov.	22	7	32	4	18
Jan.	28	12	43	1	04
Feb.	37	8	22	5	14
March	40	13	33	4	10
April	42	6	14	2	05
May	40	10	25	6	15
June	43	16	37	7	16
July	37	6	15	1	03
Sept.	77	17	22	8	10
Total	428	107	25	42	10

end of both lines are excluded from the data, the capture of unmarked animals in the last two days of trapping made up only 10 per cent of the new captures. Sixty-one per cent of all unmarked animals captured in the last two days of trapping were captured in the last ten traps on each end of both lines.

It was also desirable to use as short a trapping period as possible because trap mortality tended to increase progressively during the trapping period (Table 4).

Captured animals were toe clipped, sexed, aged, weighed, and examined for breeding condition before being released. Traps were baited with oatmeal and during the colder months corn was also placed in the traps to serve as a high energy supplement (Morrison, 1949). It was thought that the use of corn materially reduced trap mortality during the winter (Table 4). Covers, made of asphalt shingles covered with aluminum foil, shielded the traps from sunlight, rain, and snow and were thought to reduce trap mortality especially in the summer.

A ratio method was used to estimate population density. The following formula was suggested by Hayne (unpublished):

$$P = \frac{bc}{ad} \qquad (1)$$

where a is the number of animals captured in common to both lines, b the average number of animals in each of the two lines (both a and b exclude those animals dying in the traps during the trapping period), c average for

TABLE 4

MORTALITY OF MICE PER DAY OF TRAPPING

Period	Number of Mice Lost in Both Lines Day of Trapping					
	1	2	3	4	5	6
May			1			
July						
Sept.		1		1	1	1
Oct.						
Nov.		1	1			
Jan.	1		1	1	1	
Feb.						
March					1	1
April		10		1	2	
May		3		1	2	2
June	1			5	1	
July	2		2	2		2
Sept.	2	1	1	10	4	6
Totals	6	16	6	21	12	12

The total number of mice captured in one line each period may be found in Table 11.

the two lines of all captures including deaths due to trapping, $\underline{d}$ the effective area trapped, and $\underline{P}$ the population density per unit area.

The area trapped ($\underline{d}$) was greater than the square area bisected by one of the trap lines, since the home ranges of the mice extended an unknown distance beyond the lines. The square, 10,000 square meters, was increased on both sides and ends. On two sides the amount added to include the home ranges of mice coming to the line from the sides was set arbitrarily as the fraction $\frac{a}{b}$ (in Formula 1) of one-half the trap line length, 50 meters in this instance. The trap area was also increased at the ends of the square since animals caught in the traps at the ends of the lines presumably ranged beyond the trap area. Therefore, each end of the trap area was increased by a semicircle with a radius of one-half the length of the trap line plus the fractional increase computed above. Information on numbers captured and population estimates are shown in Table 11.

In calculating the production of (or total weight grown by) the Microtus population, it was necessary to use one method for the animals which were susceptible to capture (the adults and an unknown proportion of the juveniles) but to use an entirely different method for the nestling young which do not enter traps. For the trapped animals, production was calculated from the rates of growth and mortality observed with the trapped

individuals; while for the nestling young, production was inferred from the observed rate of pregnancy, the known rate of growth of young, and the calculated rate at which the young entered the trap susceptible population.

In all calculations of production, the use of instantaneous rates has been advantageous (Clarke, 1946, Clarke, Edmonson and Ricker, 1946, and Ricker, 1946). Ordinarily the objective has been to determine the instantaneous rates of growth and of mortality. Assuming constant rates, the products of these rates and the mean population for a period will yield, respectively, the production of animal tissue by the population and the quantity of tissue lost from the population. This approach is especially useful here since it allows estimation of the biomass or number of animals which were produced, grew, and were lost, between measurements of the standing crop.

The recapture of resident animals in two consecutive trapping periods allowed an estimate to be made of the rate of weight gain or loss of the individuals. This rate was estimated separately for the animals in a number of ten-gram weight classes, since the rate of growth changes with body weight (Table 15). For each weight class, the daily instantaneous rate of growth was multiplied by the mean biomass for the period to calculate the daily production by growth in that particular weight class. In some months a loss in weight was observed (Table 15).

To determine the production of the nestling young not susceptible to capture, it was necessary to establish 1. the potential production of young by the population (potential natality), 2. the number of young which entered the trap susceptible population, and 3. the growth rate of the young. The estimate of the potential production of young was based on the rate of pregnancy determined in the field and on the gestation period and litter size as reported in the literature. Pregnancy rate was established by abdominal palpation of all females. Davis (1956) suggests that 86 per cent of all pregnancies in small mammals can be determined in this manner. Although Davis's findings could probably be extended to Microtus, the percentage of adult females found to be pregnant in this study (Table 13) was so large during most of the breeding season that Davis's correction could not be made. The average number of days required for a female in the population to produce one litter could be found by dividing the gestation period (21 days, Hamilton, 1941) by the proportion of females pregnant (here termed f). With the additional information that there is an even sex ratio and five young per litter (Hamilton, 1941, Hatt, 1930, and Blair, 1940), we can infer that in each time interval of $(\frac{21}{f})$ days, one female increased to 3.5 females -the 2.5 young females plus the mother. With the use of the following formula it is then possible to calculate the production of young:

$$\frac{\frac{\ln. 3.5}{21}}{f} \times t \times p' \qquad (2)$$

where f is the percentage pregnancy among females, t is the time between trapping periods, and p' is the mean population.

The number of young entering the trap-susceptible population was assumed to equal the number of adults and juveniles lost to mortality plus the number needed to fulfill the population increase.

The growth rate of the nestling young was based on the weight increase from an assumed birth weight to the weight of the lightest juvenile captured in the live traps between trapping periods. Whitmoyer (1956) showed that the birth weight of laboratory Microtus was approximately 3 grams. The lightest weights of live-trapped juveniles ranged from 10 to 16 grams. The products of the instantaneous rate of growth of the nestling young and the mean biomass of young yielded the increase in mouse tissue due to the nestlings between the two trapping periods. The contribution of nestling young is shown in Table 16.

Food consumption by mice was studied both in the field and in the laboratory. For the field studies, wild Microtus were snap-trapped every three months in other areas which were characterized by a bluegrass-perennial herb vegetation similar to that found on the study area. At least 24 mice were captured during each trapping period (Table 23). These mice were brought into the laboratory

and their stomachs were removed and weighed. A portion of the stomach contents was placed on a glass slide with several drops of Turtox CMC-10 mounting media. A smear was made of this mixture and, after a cover glass was placed on the slide, the slide was examined under the low power objective of a microscope.

A stomach content key was devised by feeding in the laboratory five Microtus on diets of natural foods, each mouse receiving only one food substance. These animals were sacrificed and slides of their stomach contents served as a key when examining the stomachs of wild mice. Under the microscope it was possible to distinguish the following food types: grasses, herbs, woody materials, seeds, fruits, mosses, fungi, and insect remains. These identifications were made on the basis of cell shape, cell wall structure, arrangement of stomata, presence of parenchyma cells, sclerieds, tracheids, and other elements. An estimate was made of the proportion of each food type on each slide. The percentage importance of the food types were determined for the collection period by averaging the data for each individual stomach.

The quantity of food consumed was measured for caged mice in the laboratory. A total of twenty mice was used in two feeding experiments. In the first experiment, fifteen mice in five cages were fed a "standard" laboratory diet of lettuce, carrots, and oatmeal (Whitmoyer, 1956) for thirty days. In the second experiment, five mice were

maintained on fresh-cut alfalfa for thirty days. Water was available in both experiments. Animals gained weight, bred, and gave birth to normal litters on both diets. Food materials were weighed in and out of the cages daily; the weight loss of fresh food between weighings was determined by using a control cage. The information on food consumption is summarized in Table 22. The caloric value of the standard diet was determined from Wooster and Blanck (1950) and that of the alfalfa by combustion in the bomb calorimeter.

The digestibility of the experimental diets was studied by collecting mouse feces in the cages for a five day period during each experiment. The feces were oven-dried and the caloric value determined in the bomb calorimeter. By this method it was possible to estimate the amount of gross energy in the feed which was undigested.

The metabolic rate of Microtus was studied by the McLagan-Sheahan (1950) closed circuit method. This technique utilized a series of desiccator jars connected to a pure oxygen source, a vacuum pump, and mercury manometers. Soda lime, in the bottom of the jars, absorbed carbon dioxide. The system was of known volume (approximately 2600 ml.) and was kept at a constant temperature of 26°C. Wild Microtus were trapped the day before the experiment and fasted over night (12 hours). Three or four mice of the same sex and weight were placed in each jar and, after air was evacuated from the jars to

a negative pressure of 200 mm. mercury, pure oxygen was introduced until pressure returned to equilibrium. As the oxygen was consumed in the jars, the pressure changes were measured on mercury manometers. The mice were allowed about thirty minutes to become accustomed to the apparatus before readings were made on the manometers. A respiratory quotient (RQ) of .85 was assumed in the computations of metabolic rate.

Metabolic rate determined by this method can not be considered a basal rate (BMR) because the animals were slightly active in the jars during the experiments. Rather than basal rate, this study determined the fasting metabolic rate (FMR) of Microtus. The FMR (Table 18) was calculated in terms of cc. of oxygen consumed per gram mouse tissue per hour, in Calories per 24 hours per individual mouse, and as specific metabolism (Calories per 24 hours divided by weight in kilograms to the .73 power) Brody (1945, p. 369). The respiration of the adult biomass was estimated by multiplying the respiration rate in Calories per 24 hours by the population density at a trap period and by the number of days between succeeding trap periods. The product of the respiration rate of the young (assumed to be 1.7 Calories per 24 hours), the mean population of young, and the time interval between trapping periods yielded the respiration of the nestling young.

The FMR when applied to animals in the field should be considered a minimal figure of metabolism. Brody (1945,

p. 477) considered that the maintenance energy expense is twice the basal metabolic rate. The energy cost of maintenance is the net dietary energy needed to carry on life processes, excluding the production of flesh, milk, or young.

To determine the caloric value of Microtus carcasses, four wild mice were sacrificed, minced, and dehydrated in a lyophilizing apparatus. This dried material was then burned in a bomb calorimeter to determine average caloric value per gram of dry mouse tissue. The wild mice were of average weight, ranging from 10 to 39 grams, and did not exhibit large fat deposits around the internal organs.

The Least Weasel

The energetics of the least weasel were given a more superficial treatment than those of the vegetation, or of the Microtus population. Population estimates were inferred from the capture of weasels in live traps during the mouse trapping program and from counts of weasel tracks in the snow during December, January, and February. During any one trapping period, individuals were identified by weight under the assumption that only one individual of a particular weight would be present on the trap area. On the basis of trap records and tracking observations (Table 27, and page 79) it appeared that there were two adult weasels on the area of 2.5 hectares in the late fall of 1956. It was assumed that these weasels had been present and had produced young during the summer. The number of litters

produced per year (two) and the number of young per litter (five) were accepted as reported by Burt (1948) and by Hall (1951). June and August were arbitrarily chosen as the birth dates of the litters.

Growth rates of adult and young weasels was estimated from the weights of captured animals. The data in Table 27 indicated that a reasonable initial weight for the adults in the early summer of 1956 was 46 grams. These adults were assumed to have grown to an average adult weight of 60 grams by August and to have maintained this weight through the spring of 1957. It was further assumed that the birth weight of the young was three grams and that each individual in the litter grew approximately six grams per month for the first five months and then three grams per month for the next five months. As with Microtus, production measurements were based on the instantaneous rate of growth of adults and young. Production was calculated separately for three four-month periods (Table 28).

Mortality was arbitrarily estimated as approximately five young, weighing 15 grams, being lost from September to December, 1956, and one young, weighing 35 grams, being lost from January to May, 1957.

Food consumption and digestibility of food was studied in the laboratory with one captured weasel. In the course of the two feeding experiments conducted, one live mouse was placed in the weasel cage daily. The remains of the dead carcass of the mouse fed the previous day was

transferred to a hardware-cloth envelope within the cage to indicate evaporation loss from the carcass. White laboratory mice (Mus musculus) were fed in the first study and laboratory-raised Microtus in the second study. Each experiment was run for a total of 30 days.

During the feeding experiment using Microtus, feces were collected for a six day period to measure food digestibility. The caloric value of these feces was determined in the bomb calorimeter.

The metabolic rate used for the least weasel was that obtained by Morrison (1957).

RESULTS

In this study the primary concern was to determine the rate of exchange of energy, converted from solar energy by the vegetation, though the Microtus and Mustela populations. In order to accomplish this, it has been necessary to determine the rate of growth and production of young, the losses to respiration, weight loss, and mortality, and the consumption and digestibility of foods. After estimates of the monthly or seasonal energy dynamics of the populations are established, it is possible to summarize the energetics of the entire food chain on an annual basis.

Solar Energy

The annual insolation per hectare for 1956 and part of 1957 is shown in Table 5. Baten and Eichmeier (1951) indicate that the average agricultural growing season at East Lansing is from May 8 to October 4, with extremes ranging from April 8 to November 16. Field observations suggested that the growing season for natural vegetation of the old field was slightly longer than that for cultivated crops and extended from approximately April 1 (when spring plant growth became obvious) to approximately November 1 (when the accumulated production peak was reached in 1956). The total insolation during this last growing season was 94.2×10^8 Calories per hectare in 1956. Since approximately 50 per cent of the incident energy (that in the ultraviolet and infrared portions of the

TABLE 5

SOLAR INSOLATION ON THE STUDY AREA IN CALORIES PER HECTARE FOR 1956 AND PART OF 1957

Month	1956	1957
January	4.2×10^8	5.0×10^8
February	7.3×10^8	6.1×10^8
March	9.5×10^8	11.0×10^8
April	10.8×10^8	9.9×10^8
May	14.7×10^8	13.9×10^8
June	17.8×10^8	16.8×10^8
July	15.3×10^8	18.2×10^8
August	13.6×10^8	15.2×10^8
September	12.2×10^8	11.7×10^8
October	9.8×10^8	
November	4.5×10^8	
December	2.7×10^8	
Total	122.4×10^8	
Total growing season (April 1 to Oct. 31)	94.2×10^8	
Growing season correction[1]	47.1×10^8	

Data from the Michigan Hydrologic Research Station of the USDA and the Michigan Agricultural Experiment Station.

[1] 50 per cent of the total insolation during the growing season to allow for ultraviolet and infrared radiation which are not utilized in photosynthesis.

spectrum) is not used by plants in photosynthesis (Terrien, Truffaut, and Carles, 1957, and Daubenmire, 1947), the total insolation was divided by two to give the insolation available to the plants. The data presented in Table 5 represent total solar insolation at the ground surface, and at the bottom of the table is shown the 50 per cent correction of growing season insolation. This corrected insolation value is used in all calculations of efficiencies of the vegetation. The 50 per cent reduction may be excessive during April, May, and June when the total insolation at ground surface is reduced due to increased cloudiness. Clouds reduce the amount of ultraviolet and infrared radiation because of diffusion and absorbtion by water molecules (Terrien, Truffaut, and Carles, 1957) and it might be anticipated that under clouds more than 50 per cent of the insolation at the ground would be usable by the plants.

Dynamics of the Vegetation

The production of the vegetation can be separated into two different components: 1. the production of the plant tops and the root biomass over the growing season, and 2. the photosynthate which is lost due to consumption by animals and by respiration of the plant biomass. The production of tops and roots plus the material eaten by animals comprize the net production; the inclusion of the respiration yields the gross production of the vegetation.

The dry weight standing crop of vegetation (Figure 5)

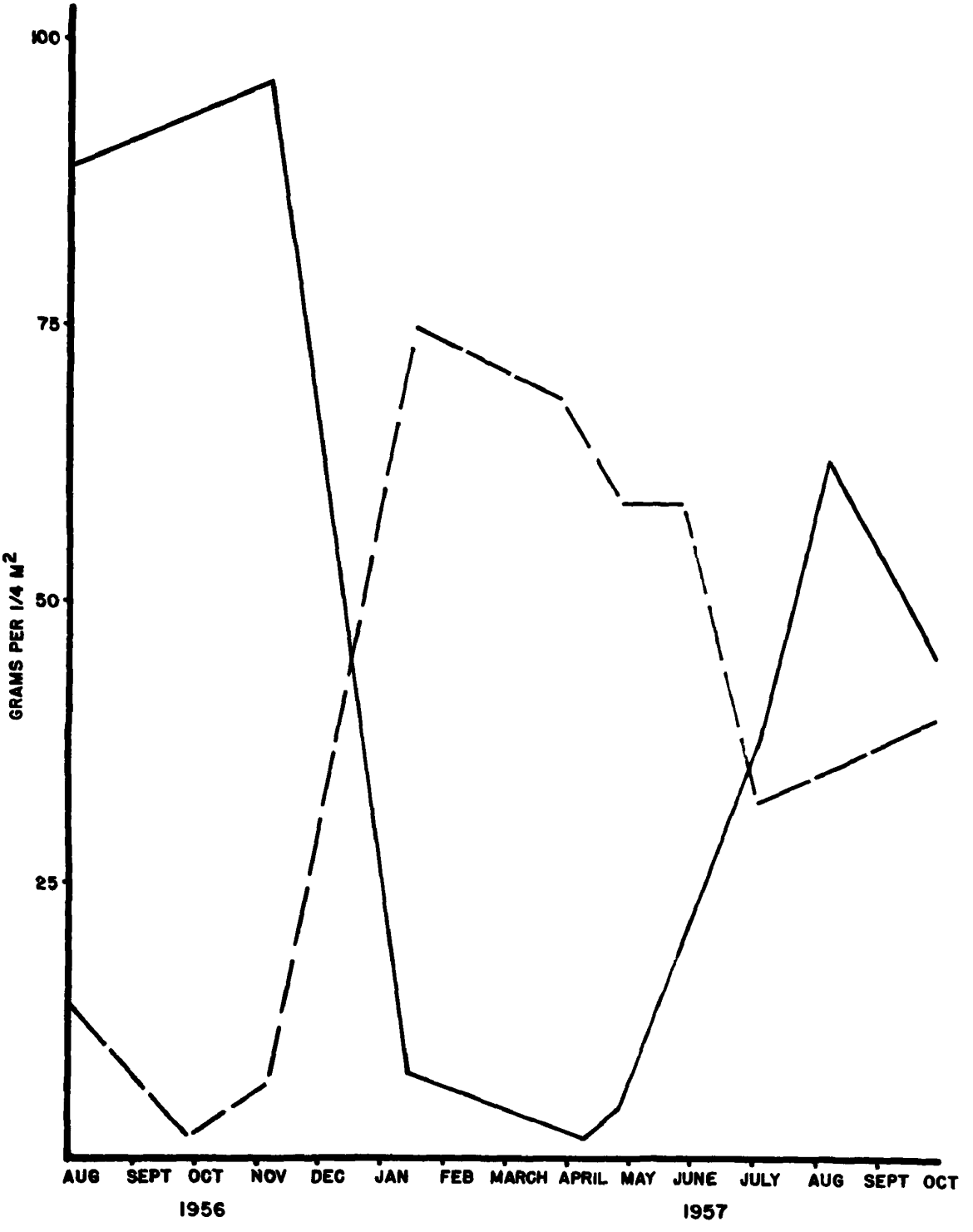

Fig. 5 - The standing crops of living (solid line) and dead (broken line) vegetation by months in 1956 and 1957.

illustrates a typical annual cycle of growth, death and decay of vegetation. The grass-herb ratio also shows cyclical flucuations; grasses predominate in fall and winter, with a tendency toward equality in midsummer. A slight change in caloric content of the vegetation also occurred seasonally (Tables 6 and 7). The peak standing crop was 385 grams per square meter (3.85×10^6 grams per hectare) in 1956 and 251 grams per square meter (2.51×10^6 grams per hectare) in 1957, these values being accepted as minimum estimates of production. The average caloric value of green vegetation was 4.08 Calories per gram dry weight (average of the values in Table 6).

Standing crop of roots was measured three times during the 1957 growing season. The initial standing crop (1493 grams per square meter, 15 cm. deep) was measured on April 13, 1957 when the vegetation was beginning spring growth. The second measurement was made on July 11, when the root standing crop was 1805 grams per square meter. The peak standing crop was 2516 grams per square meter on September 29, 1957. The difference between the peak and initial standing crop approximated the organic matter synthesized and stored in the roots above 15 cm. depth over the growing season (1023 grams per square meter) in 1957. To this value should be added an unknown amount comprized of the root hairs and root cap cells lost during the period. It was assumed that this rate was also applicable to the 1956 season. The caloric value of the roots, determined

TABLE 6

STANDING CROP OF LIVING AND DEAD VEGETATION, AND AVERAGE CALORIC VALUE OF GREEN GRASSES AND HERBS PER SQUARE METER PLOT, AND LIVING GRASS-HERB RATIO

Date Collected	Number of Plots	Standing Crop (Grams Dry Weight) Live Mean	Live s^1	Dead Mean	Dead s^1	Caloric[2] Values Cal/ gram Dry Weight	Grass:Herbs (Weight)
7/21/56	2	-	-	-	-	4.12	-
8/8/56	10	358.0	±49.2	55.6	±30.4	4.12	3.5:1
9/24/56	16	372.4	±81.2	8.0	-	4.30	9.1:1
11/2/56	20	385.2	±91.2	28.0	-	4.17	49.2:1
2/9/57	10	31.2	±12.8	300.0	±60.0	-	-
3/22/57	15	8.0	± 2.4	274	±75.2	-	-
4/24/57	14	18.4	± 6.8	234.8	±97.2	3.99	16.0:1
5/22/57	14	67.6	±12.8	236.0	±66.4	3.99	6.9:1
7/1/57	15	147.2	±49.6	126.8	±47.6	3.90	2.6:1
8/5/57	15	250.8	±71.2	140.4	±42.8	-	1.4:1
9/29/57	14	184.0	±71.2	164.0	±42.4	-	-

[1] Standard deviation

[2] Calculated from information in Table 7.

TABLE 7

THE CALORIC VALUE PER GRAM OF OVEN-DRIED PLANT TISSUE FOR VARIOUS PLANT SPECIES COLLECTED DURING THE STUDY

Date Collected	Species	Number of Samples	Calories Per Gram (Average)	Standard Deviation
7/22/56	Poa compressa	5	4.12	± .08
8/8/56	Poa compressa	9	4.18	± .20
9/24/56	Poa compressa	14	4.31	± .45
11/2/56	Poa compressa	15	4.18	± .08
5/22/57	Poa compressa	3	4.02	± .05
7/1/57	Poa compressa	3	3.99	± .11
8/8/56	Linaria vulgaris	5	4.28	± .07
9/24/57	Linaria vulgaris	5	4.34	± .10
8/8/56	Daucus Carota	5	3.92	± .45
8/8/56	Cirsium arvense	6	3.93	± .22
8/8/56	Trifolium repens	2	4.09	± .20
8/8/57	Verbascum Thapsus	3	3.98	± .14
8/8/57	Plantago spp.	2	3.79	± .09
8/8/57	Dead Grass	6	3.91	± .05
2/9/57	Dead Grass	15	4.25	± .06
4/24/57	Grass and Herbs	3	3.99	± .10
5/22/57	Herbs combined	3	3.97	± .12
7/1/57	Herbs combined	3	3.81	± .12
8/8/56	Roots	6	3.30	± .20

for a sample collected in August, 1956, was 3.30 $C_a$lories per gram dry weight (Table 7).

The amount of live vegetation calculated to have been consumed by mice during the growing seasons in 1956 and 1957 is shown in Table 25.

Data on respiration of the vegetation were collected during four nights in the summer of 1957. The CO_2 released, O_2 consumed, RQ, and Calories used per gram of plant per night are shown in Table 8. The product of the rate of respiration in Calories, the mean standing crop of vegetation and the number of days between measurements of respiration yielded the Calories used in night respiration by the vegetation over the growing season, 146.2 Calories per square meter plot or 1.46×10^6 Calories per hectare (Table 9).

Thomas and Hill (1949) in their field studies on the respiration of alfalfa showed that night respiration of the tops was approximately one-half the day respiration and that the root and combined day and night top respiration were about equal in magnitude. If we assume that these findings can be applied to the old-field vegetation, the day respiration of the tops would equal 2.92×10^6 Calories per hectare, and respiration of the roots, 4.38×10^6 Calories per hectare. Total respiration of the entire plant biomass would be approximately 8.76×10^6 Calories per hectare or 15 per cent of the total assimilation. This estimate is slightly less than those of Transeau (1926)

TABLE 8

DAILY RESPIRATION OF OLD-FIELD VEGETATION

Date	CO_2 Produced cc./night	O_2 Consumed cc./night	RQ	Calories per cc. Oxygen	Grams Vegetation[1]	Calories per Gram per Night
5/17/57	1.96	3.50	.56	.0045	.398	.041
5/25/57	1.36	1.91	.72	.0047	.589	.016
6/13/57	1.17	1.20	.97	.0050	.866	.007
7/20/57	.90	.68	1.31	.0053	1.905	.002

[1]Grams of vegetation on area covered by cans (86.6 cm^2) derived from the graph of standing crop of vegetation (Fig. 5).

TABLE 9

NIGHT RESPIRATION OF THE VEGETATION BIOMASS DURING GROWING SEASON

Date	Interval Days	Mean Standing Crop Vegetation Grams	Respiration Rate Cal/gm/night	Respiration Loss/m^2 Cal.
April 1 to May 21	51	6.1	.041	50.4
May 22 to June 2	12	16.7	.016	12.4
June 3 to July 2	30	27.6	.007	23.2
July 3 to Nov. 1	121	62.2	.002	60.2
Total				146.2

and Thomas and Hill (1949). These workers suggest that respiration of the plant biomass amounts to between 25 and 35 per cent of the total production. It is not known if the discrepancy between the estimates made in this study and those by Transeau, and Thomas and Hill is due to a diffusion of gases between the soil and air under the cans, or if it represents a real difference between the respiration of natural vegetation and cultivated crop plants.

In 1956 and 1957 the production was made up of the following components:

	1956	1957
Peak production (tops)	3.85 x 10^6gms/ha.	2.51 x 10^6gms/ha.
Root production	10.23 x 10^6 " "	10.23 x 10^6 " "
Consumed by Microtus	.01 x 10^6 " "	.06 x 10^6 " "
Weight Net Production	14.09 x 10^6gms/ha.	12.80 x 10^6gms/ha.
Caloric Net Production	49.51 x 10^6Cal/ha.	44.25 x 10^6Cal/ha.
Respiration	8.76 x 10^6Cal/ha.	8.76 x 10^6Cal/ha.
Caloric Gross Production	58.27 x 10^6Cal/ha.	53.01 x 10^6Cal/ha.

Some indication of the relative productivity of the vegetation of the old-field community can be gained by comparing the peak standing crop obtained in 1956 and 1957 with similar data for other communities (Table 10). The arctic and alpine communities studied by Bliss (1956) showed a smaller peak standing crop than most of the temperate communities included in the table. The productivity of the temperate communities could be compared by using percipitation as a basis for grouping the

TABLE 10

PEAK STANDING CROP OF VEGETATION (IN 100 KILOGRAMS PER HECTARE) OF SELECTED COMMUNITIES

Community	Source	Standing Crop
Arctic heath-tussock	Bliss (1956)	6.0
Alpine fell-field	" "	2.7 to 11.2
Calamagrostis sp.	Pearsall & Gorham (1956)	88.0
Carex sp. (ave. of 4)	" " "	49.0
Chalk grassland	" " "	82.0
Dactylis glomerata	" " "	91.0
Deschampsia caespitosa	" " "	101.0
Molinia caerulea	" " "	40.0
Pteridium aquilinum	" " "	101.0
Sphagnum sp.	" " "	68.0
Typha latifolia	" " "	107.0
Old-field (Perennial grass-herbs)	Present study 1956	38.5
	1957	25.1
Short-grass maximum	Weaver & Albertson (1956)	43.2
Short-grass minimum	" " "	5.6
Buffalo grass-blue grass	" " "	45.3

communities. The British grass-herb communities studied by Pearsall and Gorham (1956) had the highest percipitation, and the prairie grass communities of Weaver and Albertson (1956) had the least percipitation. The British communities had generally the largest peak standing crops. Although the short-grass community had the smallest peak standing crop during the drought in 1939, in general the data for the prairie grass communities were comparable with those of the old-field community.

The Dynamics of the Microtus Population

The energy dynamics of the Microtus population were separated into several components: 1. the standing crop, 2. the rate of tissue production, 3. the rate of production of young, and 4. the rate of mortality of Microtus over the year. These statistics are presented in terms of numbers, biomass, and Calories. Further, to relate the Microtus to the vegetation base of the food chain, the food consumption and digestibility of the mice was established. From this information it was possible to estimate the percentage of the available food consumed by the mice, and the percentage of the consumed food used in metabolic processes and stored as tissue production.

Standing Crop of Microtus

The standing crop of Microtus showed some unexpected variations during the investigation (Table 11). The population at the beginning of the study was at a very low level. In fact, following the first trapping program in May, 1956, an attempt was made to relocate the study on another area with a higher population of Microtus. It was not known whether this "low" was the result of adverse weather, heavy predation, or "cyclical behavior."

The estimated peak population (57 mice per acre) determined in this study could not be considered unusual for the genus. Other workers have arrived at greater estimates of population density for Microtus, as for Microtus pennsylvanicus, 118 per acre (Bole, 1939), 160-

TABLE 11

DYNAMICS OF THE MICROTUS POPULATION ON ONE HECTARE

Date	Average Number Captured Per Line	Fraction[1]	Population Density	Size of Trap Area	Average Individual Weight	Standing Crop	Mortality Between Successive Trapping Periods	
		Per Cent	Numbers	Hectares	Grams	Calories[2]	Rate[3]	Calories
May 22-28	4	29.4	5.2	2.6	29	205	75	393
July 24-30	12	41.7	9.6	3.0	29	382	37	232
Sept. 4-10	20	41.0	16.5	3.0	29	654	52	539
Oct. 9-15	19	32.4	21.2	2.7	31	898	42	710
Nov. 17-23	28	22.2	42.4	2.4	29	1685	39	1162
Jan. 6-23	22	(13.3)[4]	77.3	2.1	27	2847	27	1245
Feb. 21-27	39	13.0	139.1	2.1	29	5525	(55)[4]	3284
March 19-26	22	13.6	75.3	2.2	25	2578	35	937
April 25-1	43	30.4	53.2	2.6	32	2330	57	1931
May 23-27	39	29.4	49.8	2.6	26	1774	58	1815
June 18-25	43	26.2	65.4	2.5	28	2509	65	2544
July 29-4	34	22.9	61.4	2.4	30	2522		
Sept. 23-29	59	22.0	111.2	2.4	26	3964		

1 The percentage of total captures taken in common to both lines.
2 Caloric value of Microtus was 1.37 Calories per gram.
3 Percentage disappearing from one trap period to the next.
4 Estimated value.

230 per acre (Hamilton, 1937), 67 per acre (Townsend, 1935), and for Microtus ochrogaster, 145.8 per acre (Martin, 1956). The months in which the peak density occurred was unusual. Hamilton (1937), Martin (1956), and others showed that Microtus generally reach a peak population in the fall (September to November) after which the population decreases until breeding begins again in the spring. Linduska (1950), to the contrary, found that the peak population at Rose Lake, approximately seven miles north of the study area, occurred in January and February, a finding identical to that obtained in the present study. Linduska was unable to explain the difference between his results and those of Hamilton, but suggested that the winter peak may be a local adaptation to a xerophytic environment.

A more detailed knowledge of the population density and topography of the study area enabled the writer to suggest another explanation for the winter population high. On trap areas A and B (see Figure 1), regions of dense cover composed primarily of bluegrass sod, occurred in the center of the trap areas. These regions of dense cover may have served as places of refuge for the mice during alternately wet and freezing weather occurring in January, February, and March. The number of new captures per day of trapping was correlated with snowfall (Table 12) suggesting that snow storms stimulated increased movement of the mice. Gentry and Odum (1957) also found in Georgia that captures of the old-field rodent, Peromyscus polionotus, varied with weather

TABLE 12

SNOWFALL AND NEW CAPTURES OF *MICROTUS* IN THREE WINTER MONTHS COMPARED WITH A TYPICAL SUMMER MONTH

Day of Trapping	November		January		February		July	
	Snow[1]	Captures	Snow	Captures	Snow	Captures	Snow	Captures
1	.00	2	.00	1	.00	3	.00	4
2	.00	3	.05	1	.00	4	.00	11
3	.00	4	.01	2	.10	10	.00	4
4	.00	3	.28	8	.00	9	.00	6
5	.10	8	.17	2	.00	3	.00	9
6	.50	2	.01	1	.00	7	.00	3
7	T	0	T	2	T	1	.00	2
8			.85	11				
9			.05	0				

[1]Snowfall or sleet in inches, taken from U. S. Department of Commerce, Local Climatological Data for East Lansing, Michigan.

conditions (temperature and cloud cover). Since in November and January the increased captures of new animals occurred late in the trapping period, it was thought that these captures represented new animals moving into the trap area rather than movement of the resident population. The movements immediately before and during snowfall were considered to be due to a migration of mice from upland areas into the areas with heavier cover, resulting in an increased population on the study area during the storm periods and possibly throughout the winter.

It is also interesting to note that the fraction of animals captured in common in both lines decreased in January, February, and March (Table 11). This seasonal variation may have been the result of decreased size of the home range of the mice and consequent shorter daily movements. These in turn, may have resulted from increased density of mice or from some characteristic of winter weather acting on mouse behavior. Further information is needed before the cause for the decrease in number of captures in common in the winter can be established.

The observed fraction of animals captured in common to both lines for January (4.5 per cent) was lower than that fraction used in Table 11. The January trapping period was interrupted by heavy snowfall and it was possible to run the trap lines only three days in one period and four days in another. If the unusually low fraction .045 is used to determine population density a very high population estimate

(256 per hectare) results. It was thought that this high density was unlikely to occur since it would require a six-fold increase in the population in two months. Therefore, the fraction of common captures for the other winter months (February and March) were averaged and this average was used to estimate the January population. It has been suggested that the snow storms caused increased movement and consequently an increase in the capture of unmarked animals in January. Perhaps these animals moved elsewhere, or perhaps since the storm also interrupted the trapping program, there was little chance for these mice to be recaptured in another line before the traps were closed.

Production of Young by Adults

The potential number of young produced by thepopulation showed a consistent increase from May to November, 1956, but an irregular increase from March to June, 1957 (Table 13). The drop in production of young occurring in May, 1957 was due to the fact that a large proportion of the females in the population were juveniles (40 per cent), of these juvenile females only 6 per cent were pregnant. Actually in May, 93 per cent of the captured adult females were found to be pregnant. During January and February no females were judged to be in breeding condition and it was assumed that no breeding occurred. This assumption is consistent with the findings of other investigators (Hamilton, 1937, Martin, 1956, and Greenwald, 1957). During the first four months of the study data on the

TABLE 13

POTENTIAL PRODUCTION OF NEW MICROTUS PER HECTARE

Date	Time Interval Between Trappings Days	Pregnancy Rate Per Cent	Mean Adult Population Numbers	Potential Production Numbers	Potential Production Calories
May	64	90	7.2	24.8	102
July	42	90	12.6	28.5	117
Sept.	35	90	18.5	34.8	143
Oct.	39	90	30.7	64.5	265
Nov.	61	65	58.2	137.9	567
Jan.	35	00	104.7	-	-
Feb.	27	00	103.7	-	-
March	36	11	63.5	15.2	63
April	28	92	51.5	79.3	326
May	27	58[1]	57.8	53.8	221
June	40	78[1]	63.3	117.7	484

[1]Pregnancy rates for adult females alone were 93 per cent in May and 92 per cent in June.

breeding condition of the females were not collected. The pregnancy rate for these periods was later assumed to be approximately 90 per cent.

The potential natality suggests the maximum possible number of young which could be produced by the population, and is the source of most of the population increase and of replacements for adults disappearing from the population. The number of young entering the trap-susceptible population was assumed to be equal to the number of adults and juveniles disappearing between trapping periods. These replacement young also showed a consistent increase from spring to fall (Table 14) and in all but March and May were fewer in number than the potential production of young.

In March and May the potential production was insufficient to account for the increase in the population and/or the mortality of adults and juveniles. To account for the discrepancy between the potential production and the number of young entering the trap-susceptible population, it was assumed that mice migrated into the study area. In March and May this type of immigration was of a relatively minor nature, amounting to only 21 per cent of the mean adult population in March and 16 per cent in May. In January, however, the immigration was of greater importance since the population almost doubled between January and February (Table 11). There were no young produced in January, therefore, all of this increase must have been due to immigration. This proposition is supported by the

TABLE 14

POPULATION DYNAMICS OF NESTLING YOUNG ON ONE HECTARE

Date	Potential Production	Replacements[1]	Survival Rate	Mean Biomass of Young	Mortality		Immigration
	Numbers	Numbers	Per Cent	Grams	Grams	Calories	Numbers
May	24.8	14.5	58	144	78	107	-
July	28.5	12.7	45	135	108	148	-
Sept.	34.8	18.3	53	180	114	156	-
Oct.	64.5	38.0	59	333	176	241	-
Nov.	137.9	63.8	46	893	693	949	-
Jan.	0.0	0.0	-	-	-	-	96.0
Feb.	0.0	0.0	-	-	-	-	-
March	15.2	27.4	100	100	0	0	13.4
April	79.3	44.1	56	361	209	286	-
May	53.8	66.5	100	378	0	0	9.5
June	117.7	66.3	56	655	380	521	-

[1]Number of young replacing adults disappearing through death or migration.

previous information on the winter movements of mice immediately before or during snow storms (Table 12), which were interpreted to mean a migration of mice into the study area. It will be shown later that immigration probably occurred in all other months throughout the study.

Production of Tissue

Production of tissue in the mouse population was calculated for each trapping period from a knowledge of the average population biomass and the observed rates of growth. This calculation was carried out separately for the various weight classes, the production of tissue being estimated by methods described earlier. For each class the average biomass between times of trapping was estimated as the mean value of the corresponding population biomass determinations made at each trapping. The rates of growth were determined from weights of individual mice recaptured in two consecutive trapping periods.

On occasion certain weight classes, while obviously contributing to the population biomass, were not represented by recaptured animals, and hence, no growth rates were available for these classes. In Table 15 these instances are distinguished. Since it was known that some of the classes not represented by recaptured mice contributed to the production of tissue, it was necessary to estimate appropriate rates of growth for weight classes known to be producing tissue.

To estimate missing growth rates, use was made of the

TABLE 15

TISSUE PRODUCTION OF JUVENILES AND ADULTS PER HECTARE

Interval	Proportionate Weight Change Weight Classes in Grams				Daily Instantaneous Rate of Growth[1]		Growth	Weight Loss
	11-20	21-30	31-40	41-50	+	-	Calories	Calories
May	data not available							
July	data not available							
Sept.	2.06	1.00	1.10	-	3.08	-	74	-
Oct.	1.86[2]	1.20	1.00	.96	3.03	.19	81	5
Nov.	1.70	1.04	.82	.69	1.32	2.28	56	95
Jan.	-	.99	.86	-	-	5.15	-	123
Feb.	-	-	.94	-	-	8.20	-	152
March	1.71	1.27	.99	.91	20.92	.68	516	17
April	1.87	1.21	1.03	.91	9.92	1.72	191	33
May	1.76	1.43	1.13	.91	21.14	1.21	391	23
June	1.97	1.50	1.16	.95	24.55	.80	677	22

[1]Positive and negative daily instantaneous rates of growth derived from proportionate weight gains and losses of all weight classes within the month.

[2]Underlined growth rates were calculated by the increment method.

fact that growth rates decreased progressively with increasing weight, in each time period. This fact is obvious in Table 15 where the proportional weight changes, unadjusted for length of interval, show that over the year, the average change for mice in the 11 to 20 gram class exceeded the average change for the 21 to 30 gram class by 0.66. Similarly, the 21 to 30 gram mice exceeded the 31 to 40 gram animals by 0.30. For those classes for which information was lacking on growth rates, as detailed above, substitute values were approximated by adding the above average increment in proportionate growth to the observed proportionate change for the next heaviest weight class. For example, in October, 1956, 0.66 was added to the value of 1.20 observed for the 21 to 30 gram mice to estimate the missing value for the 11 to 20 gram animals.

In every instance survivors in the 41 to 50 gram class lost weight (Table 15). Hamilton (1941) suggests that the heavier adult mice lose weight only in the winter, but these data indicate that weight loss is characteristic of the 41 to 50 gram weight class throughout the year. This weight loss does not appear to be correlated with senility because in no instance did a heavy animal showing a weight loss disappear in the trapping period immediately following the loss in weight. Over the winter months of January and February mice in most other weight classes also lost weight. These losses are likely to occur, and probably represent the exhaustion of body fat stored over the fall months.

The weight distribution graph (Figure 6) reflected the internal dynamics of the mouse population. Since weight maybe considered a rough criterion of age, it would be expected that the greatest number of mice would fall in the lightest weight classes. However, no mice were caught in the 1 to 10 gram weight class, except in May. Whitmoyer (1956) found in his study of the growth rate of laboratory-raised Microtus that the eyes of all young were open at 11 days of age, at an average weight of 9 grams. Hamilton (1941) also showed that young Microtus did not leave the nest until they were 10 grams in weight, at 9 to 13 days of age. Therefore, it was assumed that nestling young do not leave the nest before they reach a weight of 10 grams, and that it would be very unlikely to capture an animal weighing less than ten grams in a live-trap. During the trapping program, only in May, 1957 were young mice (4) weighing less than ten grams captured.

Blair (1948) states that all small mammals old enough to leave the nest may be caught by live traps. If the probability of capture were the same for all weight classes, in those months in which reproduction occurred we would expect the highest number of captures to be in the 11 to 20 gram class. However, the 11 to 20 gram class in each month had a lower number of mice than did the 21 to 30 gram class (Figure 6). The home range of 11 to 20 gram mice may be smaller than that of the adults (McCabe and Blanchard, 1950), resulting in a lower probability of capture of juvenile mice

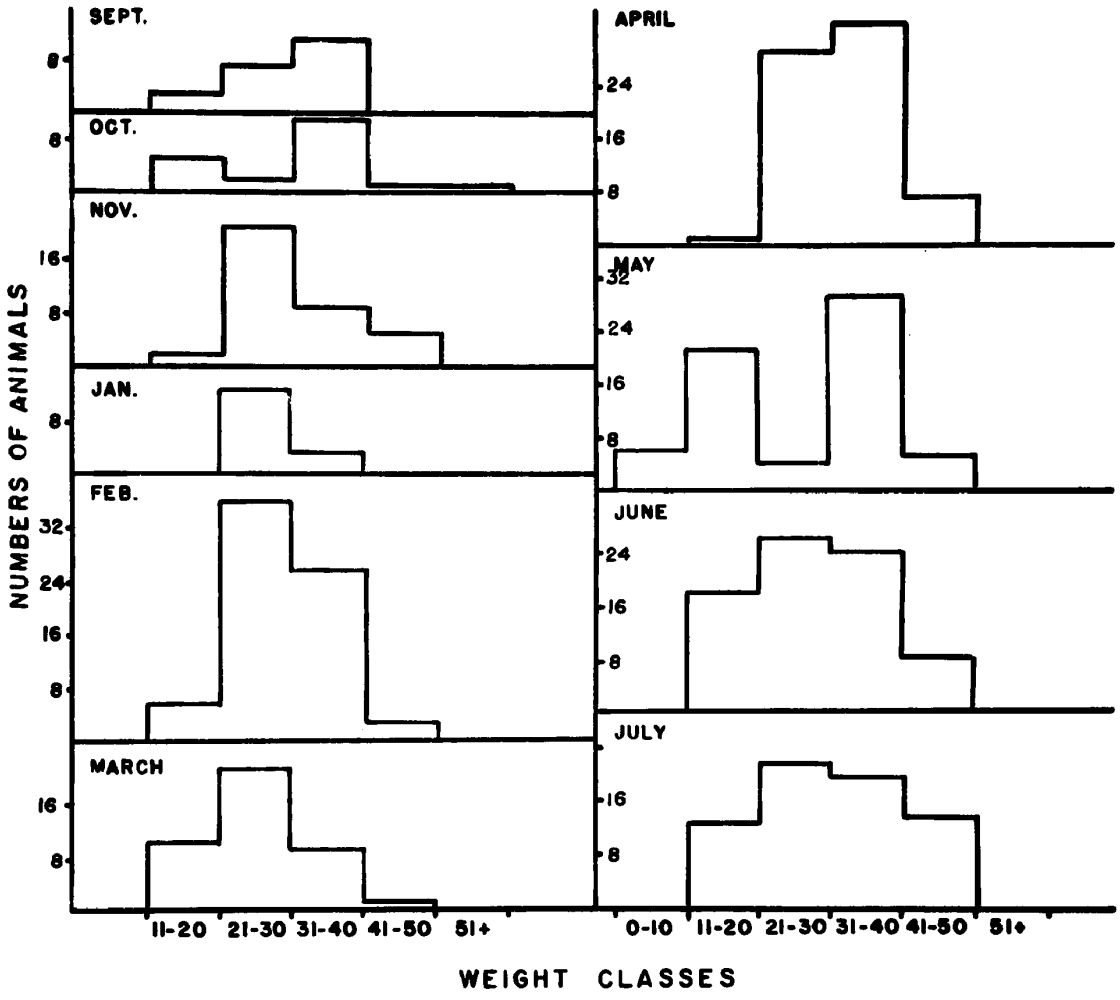

Fig. 6 - The number of animals per weight class captured each trapping period.

and a proportionately lower representation of this class of mice in the data. A second explanation for fewer animals in the 11 to 20 gram class than expected may be that the rapid growth of these mice results in their passing through the 11 to 20 gram weight class more rapidly than through the 21 to 30 gram and heavier classes. Hamilton (1941) observing the lower proportion of light-weight mice in his trapping data, suggested that exceptionally heavy mortality in this weight class may be a further cause for the phenomenon. Whatever the cause, if the probability of capture for the 11 to 20 gram mice is less than for the 21 grams and heavier animals, the determination of the biomass of the population based on live-trapping data might underestimate the contribution of the 11 to 20 gram weight class.

The growth rates of nestling young (Table 16) were generally quite similar over the year since the growth rates were calculated from a constant birth weight of three grams and the relatively constant weight of the lighest juvenile captured in the live traps. Since the nestling young had the highest growth rates, they contributed a larger share of the tissue growth or production over the period of study (Table 16) than did the adults and juveniles (Table 15).

Immigration adds energy to a population, increasing the biomass, but not by any process defined here as production. Production of these animals took place elsewhere, and hence, can not be credited to the local population, although energy losses from their respiration and mortality or emigration

TABLE 16

GROWTH OF NESTLING YOUNG PER HECTARE

Date	Mean Biomass Grams	Growth Rate	Total Growth	
			Grams	Calories
May	144	5.33	242	331
July	135	5.33	226	309
Sept.	180	5.33	302	414
Oct.	333	4.67	516	706
Nov.	893	7.67	1231	1686
March	100	4.67	154	211
April	361	3.30	435	596
May	378	4.00	524	718
June	655	5.00	1054	1444

TABLE 17

THE WET WEIGHT, DRY WEIGHT, AND THE AVERAGE CALORIC VALUE PER GRAM DRY MICROTUS TISSUE DETERMINED FOR FOUR MALE MICE

standard deviation in parenthesis

Individual	Age	Live Weight	Dry Weight	Caloric Value of Tissue	
1	adult	39.1	11.9	4.49	(± .21)
2	adult	24.5	7.0	4.67	(± .25)
3	juvenile	10.0	2.9	4.82	(± .07)
4	adult	28.0	8.1	4.63	(± .26)
average (pooled data)				4.65	(± .21)

commence to accumulate when they move into the population. For example, inspection of Tables 11 and 20 will show that immigration increased the biomass greatly during January and February, accounting for a large part of the high population metabolism or respiration.

Caloric Value of Microtus Tissue

Since the objective of this study was to determine the energy transfer and losses between the levels of the food chain, it was necessary to convert the production data, calculated initially in terms of weight, into Calories. The caloric value of mouse tissue was obtained by burning a known weight of dried tissue in the bomb calorimeter (Table 17). The mice lost approximately 71 per cent of their body weight in the drying process. Since mouse production figures were computed in terms of live weight, the average caloric value per gram of mouse tissue had to be converted from dry weight (4.65 Calories per gram) to live weight (1.37 Calories per gram). The caloric value per gram live weight of Microtus tissue can be compared with the Calories per gram edible portion of various meats, determined by Wooster and Blanck (1950):

Lean bacon	6.26	Calories	per	gram
Fresh ham	3.40	"	"	"
Rib roast	2.77	"	"	"
Round steak	1.94	"	"	"
Beef brains	1.27	"	"	"

Respiration of the Mouse Population

An estimate of the minimum number of Calories used by the mouse population in respiration was obtained from the fasting metabolic rate of Microtus. These rates showed very little variation seasonally (Table 18); an analysis of variance test of the metabolic rates of individual groups in each calorimeter jar showed that there were no significant differences in the rates between seasons or within experiments. The average metabolic rate of 10 Calories per 24 hours was used as the minimum metabolic constant to determine the minimum respiration of the mouse biomass (Table 19).

The average metabolic rate determined in the present study, in cc. of oxygen per gram per hour, compares favorably with the determinations on Microtus pennsylvanicus made by Pearson (1947), 1.9 to 2.8 cc/gm/hr, and Morrison (1948), 1.8 to 2.8 cc/gm/hr. Hatfield (1939) also studied metabolism in Microtus but arrived at a much higher figure of metabolism, 5.2 cc/gm/hr. Pearson suggested that the higher metabolic rates obtained by Hatfield were the result of the mice being active during the periods of measurement.

The metabolic rate determined by this study was a minimal rate and when used in calculations of energy loss by respiration underestimated the actual loss. The average metabolic rate of Microtus in the wild is unknown. Morrison (1948) gives some indication of what this average rate would be; in his studies, the average metabolic rate of

TABLE 18

RESPIRATION OF EXPERIMENTAL ANIMALS

Date	Ave. Weight Individuals Grams	Oxygen Consumption cc/gm/hr	Calories Per 24 Hours Per Mouse	Specific Metabolism $Cal/kg^{.73}$
Oct.	25.5	2.86	8.2	121.7
Feb.	34.9	2.55	10.6	116.0
April	31.0	2.83	10.2	128.4
Average	29.9	2.75	9.7	122.0

TABLE 19

RESPIRATION OF THE MOUSE POPULATION

Date	Respiration of Young Calories per Hectare	Respiration of Adults Calories per Hectare
May	1575	3296
July	975	4032
Sept.	1050	5758
Oct.	2329	8249
Nov.	7381	25,864
Jan.	-	27,055
Feb.	-	37,544
March	620	27,090
April	2177	14,882
May	1951	13,446
June	4544	26,160

Microtus held in the calorimeter for 24 hours, with food and water provided, was 18 to 42 per cent above the minimum rate of metabolism.

Mortality or Emigration of the Mice

Mortality and emigration both result in the disappearance of mice. When an animal was not caught again in any succeeding trap period it was not known whether the animals died or moved out of the trap area. In a few instances animals were trapped in one month and not retrapped until several months later. The question of where these animals resided in the intervening period is unanswered; here it is assumed that they were on the trap area.

The mortality of juveniles and adults was greatest immediately after the peak population was reached in February (Table 11). As was mentioned previously (page 46), this population decrease was expected to occur in December but may have been postponed by an immigration of mice into the trap area in January and February. Because of the fire on the study area in March, an estimate of the mortality rate was unavailable for February. Mortality was assumed to be 55 per cent in this period.

Summary of Microtus Energy Dynamics

The summary of the energetics of the Microtus population (Table 20) shows the energy dynamics of a population changing from a low density to a higher density. With the exception of January and February, when growth of young and adult

TABLE 20

TISSUE PRODUCTION, MORTALITY, AND RESPIRATION OF MOUSE POPULATION

IN CALORIES PER HECTARE

Period	Production		Mortality		Respiration	
	Entire Period	Per Day	Entire Period	Per Day	Entire Period	Per Day
May to July	331	5	500	8	4871	76
July to Sept.	309	8	380	9	5007	119
Sept. to Oct.	488	14	695	20	6808	195
Oct. to Nov.	787	20	951	24	10,578	271
Nov. to Jan.	1742	29	2111	35	33,245	575
Jan. to Feb.	-	-	1245	36	27,055	773
Feb. to March	-	-	3284	122	37,544	1391
March to April	727	20	937	26	27,710	770
April to May	786	28	2217	79	17,059	609
May to June	1109	41	1815	67	15,397	570
June to July	2121	53	3065	77	30,704	768
Total May to May	5170		17200		169,877	

mice did not occur, tissue production rose continuously during the spring, summer, and fall of 1956, and the spring of 1957. Mortality, comprizing the disappearance of mice from the population by death, predation, or emigration, also showed a smooth rise, with a disproportionate increase in February. The collapse of the 1956 population high occurred in March, thus inflating the mortality figure for the preceding month. Respiration was proportional to the population biomass and increased until the population drop in March. Following this, the energy loss due to respiration began a second increase.

The respiration loss, though a minimal estimate, accounted for by far the greatest amount of energy used by the Microtus population. Respiration accounted for 68 per cent of the energy passing through the mouse population yearly. In comparison, the mean biomass of mice (1900 Calories per hectare) only represented a storage at any one time of 1.0 per cent of the annual energy consumption, and the maximum biomass (Table 11) was only 3 per cent and the minimum biomass .1 per cent of the annual energy consumption.

Theoretically, since the population increased in size over the period of study, the energy lost to mortality should not exceed that appearing in tissue production. However, Table 20 shows that mortality did exceed production in every period studied. This discrepancy may be the result of several factors. First, since the standing crop increased over the year by 1569 Calories (Table 11), production plus

immigration must have exceeded mortality plus emigration by this amount. These last two processes exceeded production alone by approximately 12,000 Calories (Table 20). The conclusion follows that immigration must have been approximately 13,500 Calories. The estimates of immigration in Table 14 account only for the difference in calculated production of young and the young needed to replace trap-susceptible adults and juveniles. These estimates are included in the above calculations.

Energy leaving one population of mice by emigration joins another by immigration. Over all populations, these gains and losses must balance, just as production of all populations must equal the sum of mortality and population change. In this particular instance, immigration appears to have involved over twice as much energy transfer as production within the population itself. It is not known whether this population, sustaining a heavy predation pressure as calculated from the weasels alone, represents a "sink" with energy flowing only inward, or whether it may approach an energy equilibrium, with the weasel and other predators being in equilibrium with the local production and there being a sizable exportation of energy from the population.

A second explanation for the discrepancy between production and mortality may be that each process was calculated using different bases of computation. Production was estimated from the biomass of mice at the period of trapping, while mortality was estimated from the mean

population (numbers) of mice between periods of trapping. In the mortality calculations, a further inflation of the estimate may have arisen through converting numbers to biomass by using the mean individual weight of mice derived from the growth rate data. The mean weight of animals disappearing from the study area and those recaptured on the study area may not have been the same.

Digestibility of Food

The amount of food ingested and its energy value may be understood in relation to the metabolism of the mouse population only through some knowledge of the digestive processes and their efficiency. The gross energy in the food minus the energy in the feces equals the digestible energy (Brody, 1945). The feces include secretions and cells sloughing into the digestive tract. Thus the digestible energy indicates only the excess of food energy taken into the blood stream over excretions into the gut.

The digestibility of the food was investigated briefly in the laboratory, with results from three animals as indicated in Table 21. These interesting results are suggestive but obviously require confirmation. Such as they are, they indicate an exceptionally high digestibility for alfalfa in Microtus (90 per cent of the gross energy as against the figure of 50 per cent given by Morrison, 1949, for cattle and sheep). Further, with the diet of lettuce, carrots, and oatmeal, 82 per cent of the gross energy was digested, equalling the presumed digestive

TABLE 21

DIGESTIBILITY OF LABORATORY DIETS

Day	Caloric Intake in Food	Caloric Loss in Feces	Undigested (per cent)
Alfalfa diet - 2 female *Microtus*			
1.	128.7	20.2	15.7
2.	183.1	15.2	8.3
3.	83.3	12.9	15.5
4.	143.5	12.0	9.0
5.	176.1	12.4	7.0
average (pooled data)			10.2 (± 4.2)[1]
Standard diet - 1 male *Microtus*			
1.	26.1	4.3	16.5
2.	21.3	4.3	20.2
3.	28.9	4.4	15.2
4.	21.5	4.3	20.0
5.	23.3	4.2	18.0
average (pooled data)			17.8 (± 2.2)

[1]Standard deviation in parenthesis.

efficiency of humans with the same diet, as calculated from the tables of Merrill and Watt (1955).

Further work in this direction is needed to understand the trophic ecology of Microtus, as well as other small mammals. Attempts should be made to determine the digestibility for various single dietary components and for complete diets. The qualitative composition of the diet also requires investigation, as suggested in the following section.

Consumption of Food

The amount of food consumed, considered with digestibility, constitute the trophic levy upon the environment by the population. Food consumption may be estimated in several ways, here it has been done by laboratory means (Table 22) and by examination of the stomach contents of wild mice (Table 23).

Food consumption of Microtus has long been of interest to investigators, partly for economic reasons. Bailey (1924) fed Microtus a diet of clover, cantaloupe, grain, and seeds and found that they consumed 55 per cent of their body weight daily. Regnier and Pussard (1926) obtained similar results with Microtus arvalis on a mixed diet of oat seeds, oat stems, and mangolds. Hatfield (1935) in an experiment in which Microtus were fed a diet of dry feed (rolled oats, dry skim milk, dry meat, and seeds), found an average food consumption of 3.48 grams of food per mouse per day.

In the present study the mice on the standard diet

TABLE 22

DAILY FOOD CONSUMPTION OF INDIVIDUAL MICE ON EXPERIMENTAL DIETS

	Standard Diet				Alfalfa Diet
	Lettuce	Carrot	Oatmeal	Total	Alfalfa
Consumption grams wet weight	24.8	10.2	4.4	39.4	28.1
Consumption grams dry weight	1.3	1.2	4.0	6.5	12.0
Caloric value of food per gram wet weight	.18	.45	4.57	-	-
Caloric value of food per gram dry weight	-	-	-	-	4.1
Calories consumed	4.5	4.6	20.1	29.2	49.3
Average weight of mice (grams)				46.0	46.0
Grams food consumed per gram mouse tissue				.14	.26
Food Calories consumed per gram mouse tissue				.63	1.07

TABLE 23

WEIGHT OF STOMACH CONTENTS OF SNAP-TRAPPED MICE

Season	Number Weighed	Mean Weight of Contents	Standard Deviation	Calculated[1] Daily Food Consumption
		Grams	Grams	Grams
Fall	28	1.15	± .83	23.0
Winter	27	1.35	± .68	27.0
Spring	21	1.17	± .59	23.4
Summer	24	1.31	± .68	26.2
Average				24.9

[1]Under the assumption that the mean weight of stomach contents represents one-half the stomach capacity and that the mice have 10 activity periods per day.

consumed more fresh food than did the mice on the alfalfa diet. When dry weight of the food and caloric value was considered the reverse was true. It appears from these results and with comparison with Hatfield's findings that inclusion of dry foods in the diet reduces food consumption on a weight basis. The dry food materials (oatmeal, seed, etc.) have a much higher caloric value than fresh leafy foods such as lettuce and alfalfa, and animals on a fresh diet of succulent foods might have to consume a greater quantity of food to satisfy their energy requirements. In the present study, the mice on the alfalfa diet consumed 61 per cent of their body weight daily and those on the "standard" diet consumed 86 per cent of their body weight daily. In both instances, the food consumption as a percentage of body weight was greater than that found by Bailey (1924) and Regnier and Pussard (1926).

Since bluegrass appeared to be the dominant food plant of the environment in the study, attempts were made to maintain Microtus on a diet of fresh-cut, mature bluegrass, with water available. In two attempts most of the animals lost considerable weight, or died, as indicated below:

Trial	Number Mice	Number Dying	Number Losing Weight	Number Gaining Weight
1	6	2	2	2
2	4	2	2	0

Dice (1922) was able to maintain Microtus ochrogaster on bluegrass; possibly he fed immature grass or grass sod which might have a higher nutritive value. The energy content of

the bluegrass was 4.13 Calories per gram dry weight, which was closely similar to the caloric value of alfalfa (4.12 Calories per gram), however, the protein content of mature bluegrass (6.6 per cent, Morrison, 1949) is much lower than that of alfalfa (14.8 per cent, Morrison, 1949). Lack of protein may be the cause of the failure to maintain Microtus on a bluegrass diet. Regnier and Pussard (1926) found Microtus arvalis ate meat readily, consuming other voles and insects (Carabidae). They suggest that this consumption of protein might influence the numbers of mice during plague years. During one experiment in the present study, one Microtus was fed 8 and 7 large grasshoppers within 24 hours. Microtus may thus supplement a low protein diet with insects or other high protein foods.

The stomach contents of animals taken by snap-traps reveal the proportional composition of the diet, assuming all components to be digested at the same rate (Table 24). To infer food consumption from the information on the volume of food in stomachs, further information on the rate of stomach clearance due to digestion is required. Such information is not available. One may, however, infer from the observations of Hatfield (1940), Davis (1933), and Pearson (1947) that wild mice have characteristically 8 to 12 activity periods during a 24 hour day, and that these periods are concerned with feeding activity, to fill a near empty stomach.

The quantitative information on stomach contents (Table

TABLE 24

PERCENTAGE IMPORTANCE OF FOOD MATERIALS FROM STOMACH SAMPLES

Food Material	Fall	Winter	Spring	Summer
Number of stomachs	35	27	31	24
Grass	54	75	74	54
Herbs	28	18	23	44
Insects	T	T	1.8	T
Fruits	17	3	.1	1
Wood	1	4	.3	-
Seeds	T	-	.6	T
Moss	T	-	.1	T
Fungi	T	-	T	1
Grasses and herbs alone				
Grass	66	81	76	55
Herbs	34	19	24	45

23) may be examined, under the assumption of 10 activity periods a day, and a filling of the stomach to twice the mean observed contents at each activity period. The assumption that the mean stomach content equalled half a full stomach is supported not only by theoretical sampling considerations, but also by the observation that the observed stomachs ranged from full to almost empty, with most being "half-full."

The overall estimate of about 25 grams of food eaten per day, for all sizes of capture-susceptible mice, agrees fairly well with the laboratory-determined values of 39 and 28 grams for two different diets. It is not known if the indicated seasonal flucuations are real or reflect bias from either shifting activity patterns or changing age structure, or simply sampling variation. This method of observation does seem to offer a practical, if approximate, method of measuring food consumption.

The differential seasonal consumption of available food materials in Table 24 showed that grass (grass and sedges) was the dominant food at all seasons. Dead vegetation (with the exception of wood) was not found in the stomach slides, therefore, it was assumed that dead vegetation was not used by Microtus. Since the clip quadrats used to determine food availability and production of vegetation only sampled grasses and herbs and not mosses, fruit, and other foods, the separate percentages of grass and herbs in the stomachs were also calculated (Table 24).

The food consumption of the population was estimated by multiplying the biomass of the trap-susceptible population by the food consumption (.14 grams per gram of mouse tissue per day or .63 Calories per gram of mouse tissue per day) of laboratory mice on the standard diet. Food consumption determined with the standard diet was used because it was thought that the standard diet more closely represented the diet of wild mice. Total consumption of vegetation per trap period and the percentage of available food consumed by the mice varied seasonally (Table 25). As the population increased in midwinter, the available food decreased, resulting in a higher percentage utilization by the mice. The average utilization for the year, May, 1956 to May, 1957, was .41 per cent. Considering the growing season alone, the mice consumed more food in 1957 than in 1956 because there were more animals in the second season (Table 26).

TABLE 25

UTILIZATION OF AVAILABLE FOOD BY MOUSE POPULATION

Date	Food[1] Consumed Calories	Food Available Calories	Food Utilized Per Cent
May	5510	3.11×10^6	.18
July	6683	7.50×10^6	.09
Sept.	9568	15.65×10^6	.06
Oct.	14,639	16.00×10^6	.09
Nov.	42,832	11.60×10^6	.37
Jan.	41,726	2.35×10^6	1.78
Feb.	62,220	$.84 \times 10^6$	7.41
March	38,710	$.49 \times 10^6$	7.90
April	27,223	$.73 \times 10^6$	3.73
May	19,969	2.71×10^6	.74
June	41,845	4.38×10^6	.96
Total, May to May	249,111	60.98×10^6	.41

[1]Caloric value of vegetation consumed was assumed to be 4.08 Calories per gram.

TABLE 26

FOOD CONSUMPTION OF MICROTUS POPULATIONS DURING THE 1956 AND 1957 GROWING SEASONS

Date	Interval Days	Density, Mice Per Hectare	Individual Mean Weight Grams	Population Biomass Grams	Consumption Grams Per Hectare
1956					
April 1	52	5.0	29	145	1056
May 22	63	5.2	29	151	1329
July 24	42	9.6	29	278	1634
Sept. 4	35	16.5	29	479	2349
Oct. 9	22	21.2	31	657	2024
Total					8392
1957					
April 1	53	64.2[1]	32	2054	15,243
May 23	26	49.8	26	1295	4,714
June 18	36	65.4	28	1831	9,227
July 24	61	61.4	30	1842	15,732
Sept. 23	38	111.2	26	2891	15,379
Total					60,295

[1]Average of March and April population estimates.

The Least Weasel Population

During the study least weasels were captured in 15 live-traps and were tracked on three different days during the winter. The largest number of individuals captured in one trap period was four in May, 1957. Examining the entire area for tracks on three days in winter (in each instance the morning following a snowfall of the previous day) resulted in tracks of one weasel seen in December, two in January, and three in February. According to Polderboer (1942) the maximum home range of the least weasel is two acres. Since the study area averaged 6.2 acres in size, it was assumed that three or four adult weasels could live on the area. Although the first evidence of weasels was not noted until July, 1956, it was assumed that two weasels were present at the beginning of the study in May, 1956.

Burt (1948) states that two litters of young are born per year and Hall (1951) states that the weasel may reproduce throughout the year. Litter size ranges from four to ten (Burt, 1948) and averages five (Hall, 1951). The scatter of weights of captured weasels shown in Table 27 suggest that at least two litters of young were produced this year. If two litters of five young were produced by the weasels over the year, it was estimated that approximately ten weasels were present on the area in September, 1956. This population of ten animals could decrease to six animals in May, 1957. The mean weight of the young dying in the period August to December was estimated at 15 grams, and in January

TABLE 27

TABULATION OF LEAST WEASEL TRAPPING DATA

Date Captured	Trap Number	Weight	Sex
7/27/56	A-35	-	-
9/8/56	A-36	-	-
1/6/57	A-6	61	-
2/25/57	A-8	-	-
4/29/57	C-37	46	-
4/30/57	D-39	62	♂
2/11/57	A-5	-	-
2/11/57	A-45	28	♂
5/26/57	D-39	65	♂
5/28/57	C-34	52	♀
5/28/57	D-20	44	-
5/29/57	B-46	37	♀
7/29/57	B-6	71	♂
7/29/57	B-15	39	♀
9/26/57	D-21	56	-

to May as 35 grams. Although the population estimates may appear unusually high since the least weasel has been considered a rarity in Michigan (Hatt, 1940), all evidence supports the figures.

Under the assumption that the population of least weasels followed the model developed in the section on methods and further elaborated in the the above introductory paragraphs, the production of tissue by the weasels remained rather steady throughout the year (Table 28). In the summer, production of tissue was due to growth of both adults and young. In the fall and winter, the population of young, decreasing from 10 to approximately 5 animals, contributed all of the growth in this period. In the late winter and spring, the population of young, decreasing from five to four animals, again furnished all of the growth of tissue.

The respiration energy loss of the weasel population, based on an average minimum rate of oxygen consumption of 1.61 cc. Oxygen per gram per hour (Morrison, 1957), increased over the year of study (Table 28). As observed with Microtus, the energy used in respiration of the weasel biomass was considerably greater than that involved in tissue production.

The laboratory feeding experiments were used to evaluate the role of the least weasel as a predator on Microtus. Microtus were assumed to be the sole food used by the weasel (Hatt, 1940). This aasumption may be somewhat in error, since Blarina brevicauda, which existed in moderately large numbers on the area, and insects, which were in abundance during the

TABLE 28

DYNAMICS OF LEAST WEASEL POPULATION ON ONE HECTARE

Season	Average Population Number		Total Biomass Grams		Proportionate Weight Change		Production Grams		Mortality Grams		Respiration Loss Calories
	Adults	Young	Adults	Young	Adults	Young	Adults	Young	Adults	Young	
May-Aug.	.80	2.0	42.4	10.3	1.30	2.58	11.1	10.0	0.0	0.0	1091
Aug-Dec.	.80	2.8	48.0	34.9	0.00	3.04	0.0	38.8	0.0	31.5	1884
Jan-May	.80	1.6	48.0	61.9	0.00	1.76	0.0	35.5	0.0	10.5	2459

summer, might also have served as food for the weasels. In the laboratory experiments, the captive weasel consumed 15.1 grams of white mice or 14.7 grams of Microtus per day (Table 29). Llewellyn (1942) found a similar consumption in studies with a 32 gram weasel, ie. 19.7 grams of mice per day. An average food consumption of 15 grams of mouse tissue per day assumed to represent the true food consumption of adult weasels over the year. The young weasels, like other animals (Morrison, 1949), would probably use less food per day than the adults, and the daily food consumption of young was estimated to be 5 grams per day from May to August and 8 grams per day from August to December. Using these constants as a basis for calculating true food consumption, the effect of the weasel on the Microtus population was estimated. The weasel population consumed 5824 Calories annually; this consumption was 3.07 times the mean biomass of Microtus (1900 Calories) over the year. Since net production of the Microtus population only totaled 5170 Calories per hectare annually, the weasel population appears to have required energy in excess of that produced by its principal prey. As previously noted, the production of the Microtus population did not allow for the energy imported by mice which moved into the area. Further, it is possible that the weasels had other sources of food, or perhaps the calculations of weasel population density here are in error.

The percentage of the energy in the mouse carcasses which was digested by the least weasel was determined in the

TABLE 29

FOOD CONSUMPTION OF THE LEAST WEASEL FED ON LIVE MICE

Species	Food Consumption Grams	Calories	Caloric Value of Feces	Per Cent of Food Digested
Microtus	14.7	19.99	2.02	89.9
White mice	15.1	29.50	-	-

TABLE 30

EFFICIENCY OF CONVERTING FOOD TO GROWTH AND TOTAL METABOLISM BY THE WEASEL

Period	Food Consumed Calories	Production Cal/ha.	Per Cent Used in Production	Total Metabolism Cal/ha.	Per Cent Used Total Metabolism
May-Aug.	1136	29	3.78	1120	98.77
Sept-Dec.	2324	53	2.28	1937	83.34
Jan-May	2364	48	2.63	2507	106.05
Total	5824	130	2.23	5578	95.77

digestibility experiments. When the weasel was on the Microtus diet, he was able to digest 89.9 per cent of the energy in the mice bodies (Table 29). This rather high efficiency of digestion is comparable with the somewhat lower efficiency of digestion (70 to 80 per cent on a dry-feed diet, McCay, 1949) for the dog.

The efficiency of the weasel in converting the energy consumed in the food into weasel tissue (net production) was quite low (Table 30). Comparable information on the food conversion efficiency of terrestrial carnivores is not available. Odum (1957) showed that in Silver Springs, an aquatic community, the efficiency of converting ingested food to net production at the carnivore level was 17 per cent.

The efficiency of converting the energy consumed in the food into total metabolism (net production plus respiration) in the present study was exceptionally high. Since it would be expected that there would be other losses of energy in the animal body besides that pertaining to respiration, this high efficiency should probably be considered incorrect. An additional reason for not accepting the estimate of the efficiency of conversion of food to total metabolism is that in one period total metabolism accounted for more energy than was consumed.

DISCUSSION

In the transition of energy between two steps of the food chain there are to main pathways by which energy can be lost or diverted from the food chain itself. First, in tracing the energy from one population to the next not all the food organisms will be consumed by the consumer species; some of this energy could be dispersed to another food chain by migration of the food species out of the study area, by consumption of the food species by organisms outside of the food chain, or by death with consequent freeing of energy. Second in considering the energy consumed by the organisms in the population not all the energy consumed is used in growth or in production of young. Some of this energy is diverted to the maintenance of the organism and some passes through the body unused. In energy losses of the first order mentioned above, the energy lost from the immediate exchange is still in a form available for use by other animals. In energy losses of the second order, the loss is primarily heat derived from metabolic processes which is unavailable for further use by the food chain; that passing through the body is available to various other organisms in the food web.

Energy Losses of the First Order

Of the solar energy available to the vegetation over the growing season (one-half of the total insolation), 1.2 per cent was utilized in the gross production, and 1.1 per cent in the net production of the vegetation (Figure 7).

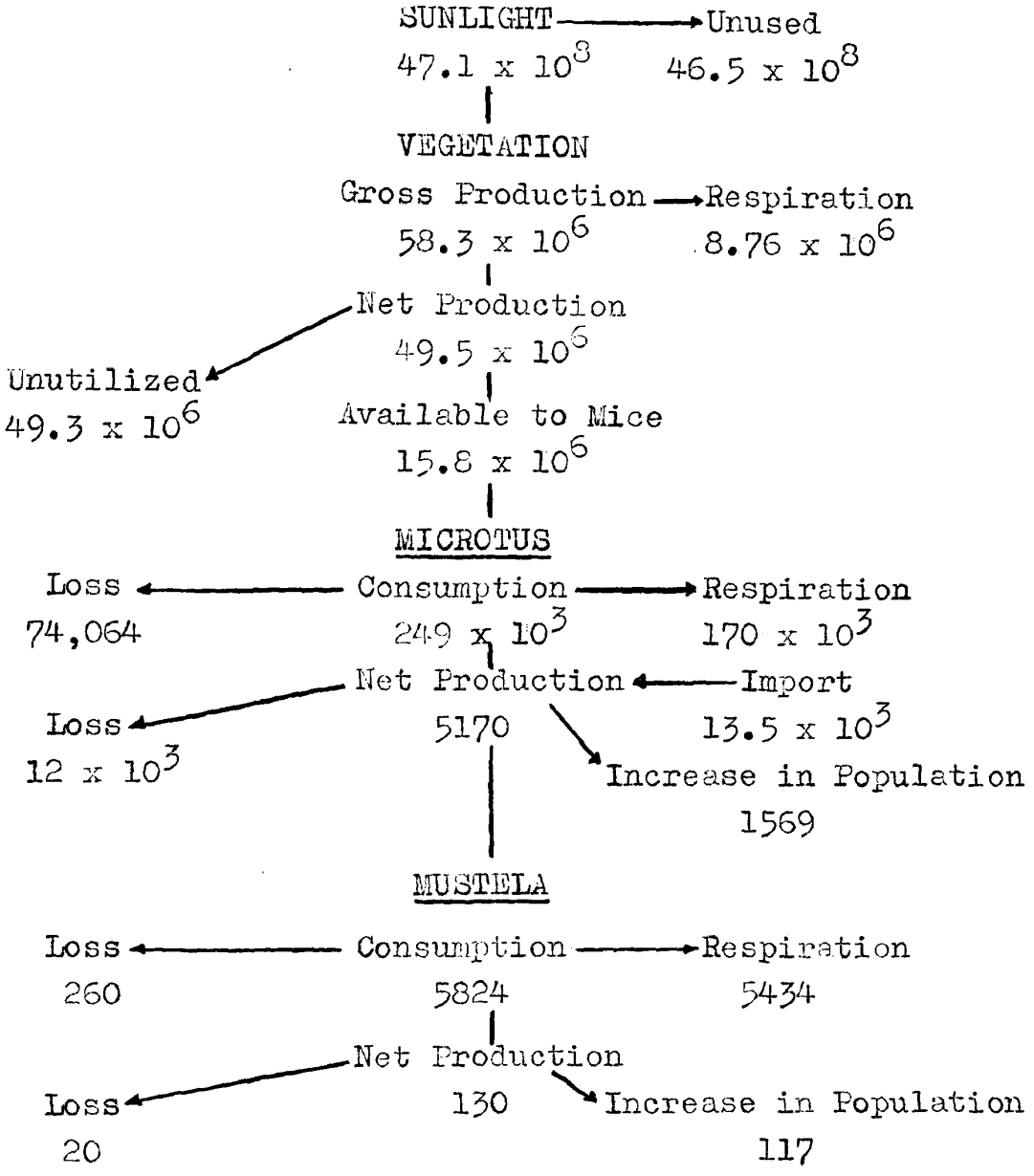

Fig. 7 - The energy flow through the food chain from May, 1956 to May, 1957 on one hectare. All figures are Calories per hectare.

These figures can be compared with Lindeman's (1942) 0.1 per cent (Cedar Bog Lake) and Juday's (1940) 0.4 per cent (Lake Mendota). Ivelev (1945) points out that these percentages should also be compared with those for highly productive agricultural practices during the vegetative period (1.6 per cent, Transeau, 1926, and 2 to 3 per cent, Doiarenko, 1925). Data on the percentage of solar energy utilized by the vegetation of different communities are still too limited to allow any comparison of the efficiencies of a successional community with a stable community or between the vegetational components of the various major climatic belts. At this time we may say only that terrestrial vegetation of the old-field community on this soil, at this site, and for these years appears to utilize approximately one per cent of the available solar energy during the growing season.

The net production of the vegetation can be considered as the energy available to the herbivorous animals in the community. Microtus is primarily a herbivore, with animal food appearing only in trace amounts over the year (see Table 24). It was assumed in this study that all green above-ground vegetation could be utilized by Microtus. Some of the root biomass was undoubtedly also used by the mice, but no estimate of the extent of root utilization was available. Lantz (1907) and Bailey (1924) state that consumption of roots is relatively unimportant, except during the winter, and roots were not recorded among the

stomach contents in the present study. It is assumed here that use of roots was negligable.

Of the energy in the vegetation presumably available to the mice (Figure 7), 1.6 per cent was consumed, with 1.1 per cent utilized by the mice in growth and respiration. These percentages assume no loss of vegetation due to cutting of stems and leaves by Microtus. The utilization of the energy in the vegetation not consumed by mice was not traced further in this study. Some of this energy was probably diverted through invertebrate food chains. Wolcott (1937) indicated that insects ate $.94 \times 10^6$ grams (3.76×10^6 Calories) of above-ground vegetation per hectare in a pasture in New York over the summer. This level of consumption would amount to 23.9 per cent of the available energy in the old-field vegetation of the present study. If these data are correct, insects may be considered as more important herbivores in the old-field community than are the meadow mice.

As mentioned previously, the energy in the Microtus population (net production) available to predators was augmented by an import of energy through immigration of mice into the study area. This immigration was particularly noticable in the winter and spring of 1957. Of the total energy available in the Microtus population (net production plus immigration, Figure 7) the least weasel consumed 31 per cent as food and used 30 per cent in growth and respiration; considering only the net production of the mice, the weasel

consumed over 100 per cent. When the energy consumed by the weasel and the energy retained in the mouse population through an increase in population size from May, 1956 to May, 1957, was subtracted from the net production plus energy imported through immigration, 43 per cent of the energy was unaccounted for. This loss may be attributed to emigration, to death from disease or accident, and degradation through microorganism food chains, or to capture in other predator chains. Some possible predators are Blarina brevicauda (Eadie, 1952), Felis domesticus (Toner, 1956, and Korschgen, 1957), or owls, red-tailed hawks, red-shouldered hawks, and coopers hawks (Kirkpatrick and Conaway, 1947, Linduska, 1950, and Hatt, 1930). All of these predators were seen on the study area during the investigation.

Most of the calculated net production of the weasel population could be accounted for by the increase in the size of the population from May, 1956 to May, 1957. Only 10 per cent of the net production was not accounted for. (Figure 7). The least weasel may itself serve as food for certain predators, such as the great-horned owl, the barn owl, long-tailed weasel, and domestic cat (Hall, 1951) but no information was gathered on mortality of weasels during this investigation.

Energy Losses of the Second Order

The energy losses of the second order, due to respiration at rest (fasting metabolism), nonassimilation of energy in the food, and the energy cost of maintaining the body under

normal activity, can be further separated into energy losses available to and unavailable to the biosphere. Energy losses available to the biosphere include the energy in fecal matter which is composed primarily of unassimilated food but also contains intestinal secretions and cellular debris. Energy in the feces would serve as the base for food chains of coprophagous organisms. The energy lost to the biosphere as heat energy derived from animal metabolism can be considered an increase in the positive entropy of the ecosystem.

Respiration loss (respiration energy/energy consumed) determined for each step of the food chain is shown below:

Vegetation	15.0 per cent
Mice	68.2 per cent
Least Weasels	93.3 per cent

The respiration coefficient for the vegetation may be underestimated as stated earlier; Transeau (1926) and Thomas and Hill (1949) suggest that it may run as high as 25 to 30 per cent. The data do confirm the statement of Lindeman (1942) that as energy passes through the food chain an increasing amount is lost in respiration. It must be remembered that the percentages cited above for the mice and weasel were both determined as minimum metabolic rates and, therefore, indicate basic differences in the loss due to metabolism and not mere differences in activity. Taking activity into account would presumably act to increase the difference.

The energy consumed but not assimilated by Microtus and Mustela was measured in the digestion trials. Of the energy consumed, 10 to 18 per cent was recovered in the feces of Microtus and 10 per cent in the feces of Mustela.

When these losses were subtracted from the energy loss of the second order for each species, 14 to 22 per cent of the energy consumed was unaccounted for in Microtus and all the energy loss was accounted for in the least weasel. It is highly unlikely that the energy loss in respiration and in the feces comprize the total energy losses in the organism. For instance, energy is also lost in the urine, in fermentation gases, and in the specific dynamic action of feeding. Estimates of the loss in the urine are 15 per cent for cattle and 7 per cent for rabbits after fecal losses are subtracted from the gross food energy (Brody, 1945, p. 28), and the loss in specific dynamic action varies from 40 per cent of the intake energy for lean meat, 15 per cent for fat, and 6 per cent for sucrose (Brody, 1945, p. 61).

An additional energy loss not included above is the expense of normal body activity above rest. Very few investigators have been concerned with this maintenance cost according to Brody (1945), although he estimates that this loss is twice the basal metabolic rate. The minimum energy expended when the animal is at rest (fasting metabolism) is known for Microtus and Mustela and was used to determine the loss of energy in respiration; but the energy used by these animals as they live in their natural

environment is completely unknown. This latter energy expense reduces the efficiency of conversion by widening the gap between energy intake and net production. The maintenance losses are reflected in the efficiencies of production (net production/energy intake). Plants are the most sedentary and have the highest efficiency, 94.3 per cent (net production/gross production). The weasel is the most active, since it must hunt for its food, and probably has the highest maintenance cost, with a low efficiency, 2.2 per cent (net production/energy intake). Possibly the energy expense of hunting by the predator will vary with different densities of the prey population. Microtus which is primarily dependent on vegetative material could be expected to have a low cost of maintenance and to display a higher efficiency than that shown in the study (2.1 per cent).

Since the maintenance cost is irreducible, the efficiency of converting energy to production will be highest when the birth of new animals and the growth rate of living animals are the highest. This surge of production can most easily occur when sources of high energy food are available. Microtus conforms to this model, since the young are born and the rate of growth is highest during the periods of greatest growth of the vegetation.

From experiments of several investigators, including Baker and Ransom (1932), it appears that increasing day length stimulates Microtus to begin breeding. The question

arises whether this photoperiodism may not be an adaptation to the accompaning growth of the vegetation (energy source of the mice) rather than being directly related to increased day length of itself? It would further increase the year-around efficiency of the population to have the lowest population density during the period of little or no production by plants since at that time the dangers of over-exploitation of the food supply would be greatest. This is the usual observation in field studies of the population dynamics of Microtus (Blair, 1940, Martin, 1956, Greenwald, 1957, and others).

The total energy losses of the second order, when the hypothetical maintenance cost is added to the known losses in respiration and in the feces, plus the net production would total more than the energy consumed for both the Microtus and Mustela populations. The reasons for this discrepancy were not determined, but food consumption rates estimated in the laboratory likely underestimate the true food consumption of the more active animals in the field.

SUMMARY

The energy dynamics of the perennial grass-herb vegetation - Microtus pennsylvanicus pennsylvanicus Ord - Mustela rixosa allegheniensis Rhoads food chain of the old-field community was studied from May, 1956 to September, 1957. Solar insolation for the growing season, measured at East Lansing, totaled 94.2×10^8 Calories per hectare in 1956.

Primary net production was broken down into the following components: 1. production of tops, 2. production of roots, and 3. consumption by Microtus. The net production for 1956 was 49.5×10^6 Calories per hectare and for 1957 was 44.3×10^6 Calories per hectare. Respiration of the vegetation during the growing season ammounted to approximately 15 per cent of the net production, determined by crude field calorimetery. Gross primary production ranged from 58.27×10^6 Calories per hectare in 1956 to 53.01×10^6 Calories per hectare in 1957.

Population dynamics and weight changes of the Microtus population were studied by live trapping. Tissue production of young and adult mice was 5170 Calories per hectare per year. The fasting metabolic rate of mice determined in the laboratory was approximately 10 Calories per mouse per day. Calories lost to respiration equalled 169,877 Calories per hectare per year. The total Calories used in growth of the weasel population were 130 Calories per hectare per year and in respiration, 5434 Calories per hectare per year.

Stomach sample analysis indicated that Microtus ate

primarily green grass and herbs. Weasels were assumed to feed predominantly on Microtus. Total yearly food consumption on the study area as determined from laboratory experiments, was 249,111 Calories per hectare for Microtus and 5824 Calories per hectare for Mustela.

Of the solar energy available during the growing season, the vegetation used 1.2 per cent in gross production, and 1.1 per cent in net production. These results compared favorably with the coefficients for primary production of terrestrial and aquatic communities determined by other workers. Of the energy available to the mice, 1.6 per cent was consumed and 1.1 per cent was utilized in growth and respiration. The weasel population consumed 31 per cent of the energy available to it in the form of Microtus, and used 30 per cent of the energy consumed in growth and respiration.

Twenty-one per cent of the net production of the Microtus population and only 10 per cent of the weasel net production was lost from the food chain. These losses were diverted to other food chains through other predators or through micro-organisms.

Of the energy consumed only a portion was used in production; most of the energy went to respiration and to maintaining normal activity, or passed through the digestive tract unused. Respiration cost increased from the vegetation level to the carnivore level of the food chain. The gross energy in the experimental diets which was recovered in the feces amounted to 10 to 18 per cent for Microtus and 10 per cent for Mustela.

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