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Predator
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.....
UNIVERSITY..... Carleton University
DEGREE FOR WHICH THESIS WAS PRESENTED..... Ph.D.
YEAR THIS DEGREE GRANTED..... Spring, 1972.

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DATED... 20 June 1972

NL-91 (10-68)

THE ECOLOGICAL ENERGETICS
OF A HOMEOTHERMIC PREDATOR

by

JAMES COLLIER RANDOLPH, B.A., M.A.

A thesis submitted to the Faculty of
Graduate Studies in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

Carleton University

Ottawa, Ontario

November, 1971 [i.e. 1972]

The undersigned hereby recommend to the
Faculty of Graduate Studies acceptance of this thesis,
submitted by James Collier Randolph, B.A., M.A., in
partial fulfilment of the requirements for the degree
of Doctor of Philosophy.

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ABSTRACT

Seasonal variations in the thermal energy environment of an animal population may cause variations in the chemical energy flow through the population. A detailed examination of the thermal and chemical energy fluxes of an individual predator was used in estimating the energy transfer from prey populations to predator populations on a seasonal basis. The short-tailed shrew, Blarina brevicauda, was selected as the predator because it is a homeotherm which is active during the entire year.

Shrews were trapped both during summer and winter; experiments utilized freshly-caught animals from both seasons. Food consumption, fecal and urinary production, oxygen consumption, and fur surface temperature were examined as functions of different thermal energy fluxes. Chemical energy was measured by bomb calorimetry. In addition to laboratory studies at different controlled temperatures, naturally-occurring temperatures and net radiant energy fluxes were recorded, summer and winter, at several locations in shrew habitat. Prey abundance, prey activity, shrew food consumption, and shrew activity were investigated with respect to these temperatures.

Currently existing models of assimilation and heat transfer in animals were utilized as subsystem components in a deterministic model, which was designed to be primarily descriptive and secondarily, predictive.

Blarina has a combination of metabolic, insulative, and behavioral adaptations that allow its survival through a wider range of environmental temperatures than occur annually in its typical habitat. Both insulative and metabolic modifications occur seasonally. Within the range of 0° to 25° C, Blarina metabolism is inversely proportional to ambient temperature. At the same ambient temperature heat loss is lower from winter shrews than from summer shrews. Winter shrews at winter temperatures have a higher metabolic rate than summer shrews at summer temperatures.

Blarina has a digestive efficiency of about .90 and it is not affected by seasonal temperature changes. Changes in the thermal environment have a more pronounced effect on a shrew's prey energy requirement than do changes in the daily level of locomotor activity. Blarina's metabolic rate during normal, exploring locomotor activity is approximately double that during sleep.

Assuming the population energy budget is represented fairly accurately as an aggregate of individual energy budgets, the model estimated that the winter food requirement of the predator population is about 43% higher than the summer food requirement. A population of 20 Blarina in a 6.47 acre deciduous woodlot near Manotick, Ontario would require only about 3% of the total prey energy base during the summer and about 37% of the prey energy base during the winter. The prey energy available per square meter of forest floor during the summer is estimated to be about 8 times the prey energy available per square meter during the winter. A population of 20 adult Blarina should experience little difficulty in obtaining sufficient food both during summer and winter.

ACKNOWLEDGEMENTS

Dr. Polley Randolph offered a great deal of encouragement and assistance. She deserves a sincere and very special "Thank you."

I gratefully acknowledge the support and guidance of Dr. H.G. Merriam. His high standards make him a very influential supervising professor. Dr. C.A. Barlow has given much assistance and advice, for which I am very thankful. For helpful discussions and suggestions, I wish to express my appreciation to the other members of my committee, Dr. S.L. Jacobson and Dr. J.S. Hart, National Research Council.

Other faculty members in the Department of Biology who have offered equipment and information include Drs. D.A. Smith, M.B. Fenton, E.M. Arnason, J. Sinclair, and J.A. Webb. Dr. T.J. Ryan, Department of Psychology kindly allowed me to use a mobile laboratory.

A.A. Raffler and the staff of the Science Workshop were very helpful in constructing experimental apparatus. Cliff Wilson and Do van der Weyden also offered technical assistance.

I thank H.B. MacCallum, manager of Glenacres Farms Ltd., for permission to do field work in the Manotick woodlot.

Dave Thomas, Carleton University Computer Center, encouraged the usage of the Sigma 7 computer.

Larry Didow assisted in trapping and contributed many ideas in our frequent discussions. Other fellow students who have helped in various ways are: Lianne Mack, Keith Hay, John Dixon, Galen Greer, Doug MacDonald, Jim Patterson, and Greg Weary.

I express my sincere appreciation to my parents for their support, interest, and encouragement in the continuance of my education.

J.C.R.

November 1971

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INTRODUCTION

Energy is defined as the capacity to do work. Work is defined as the product of a force acting through a distance. Various forms of energy are recognized, but those of greatest importance to living organisms are mechanical, chemical, radiant, and thermal. The sun releases radiant energy by the nuclear fusion of hydrogen atoms to helium atoms. Solar energy reaches the earth's atmosphere at a rate of $2 \text{ cal/cm}^2/\text{min}$ (Gates, 1962). The radiation penetrating the atmosphere is attenuated exponentially by atmospheric gases, dust, water vapor, and cloud cover. The downward flow of radiation includes direct solar, diffuse sunlight scattered by the clouds and sky, and thermal infrared radiation from the atmosphere and clouds. The upward flow of radiation includes reflected sunlight from the surface and thermal infrared radiation from the ground. The net radiation at the surface, which results in a gain or loss of energy, will evaporate moisture, or create air density gradients, resulting in winds. Gates (1962) emphasizes that all living organisms live in a thermal radiation environment which may be modified by solar radiation, convection, and latent heat exchange.

Through the process of photosynthesis the nuclear reactions occurring on the sun supply the vast majority of biological energy on the earth. Some organisms are capable of utilizing materials with a low chemical potential energy; however, the contribution of these chemosynthetic autotrophs is insignificant compared with that of photosynthetic autotrophs. Only a very small amount of the radiant energy absorbed by plants is utilized to produce chemical energy. It has been estimated from the output of fixed carbon by a field of corn in one growing season, that only 1 to 2% of the radiant energy falling on the field is recovered (Lehninger, 1965). Photosynthesis consists of the absorption of radiant energy by chlorophyll, the conversion of the absorbed light energy into chemical energy, and the utilization of this chemical energy for the reduction of carbon dioxide to form glucose. Some of the glucose will be oxidized by the plant to CO_2 and H_2O to provide energy for its own respiration. The glucose that is formed in photosynthesis may be converted in other enzymatic reactions into other products such as cellulose, proteins, and lipids.

Heterotrophic organisms require these high-energy products of photosynthesis. The chemical energy released during the combustion of food is utilized to do work. All living organisms do internal work to stay alive and most organisms also do work on the environment. All forms

of work lead to dissipation of energy to the environment. When an animal takes in chemical energy, a large part is converted to heat and a small part is stored in the chemical energy of new protoplasm.

Because all forms of energy can be converted completely to heat, but not completely to any other form, the calorie, as a measure of heat, is especially useful for comparative purposes. Chemical energy can be measured in calories as the heat of combustion by means of a bomb calorimeter. Scott (1965) outlines procedures by which a measure of enthalpy (ΔH) could be determined for biological materials from heat of combustion. The change in enthalpy is measured by

$$\Delta H = \text{heat of combustion} + \Delta nRT \ln(P_1/P_2)$$

where, R is the gas constant

Δn is the change in the numbers of moles of gas during the reaction

P_1 is the final pressure in the bomb

P_2 is the initial pressure in the bomb

T is the absolute temperature.

However, the correction to constant pressure ($\Delta nRT \ln(P_1/P_2)$) is less than the accuracy of the bomb calorimeter ($< 1\%$). The heat of combustion is then a measure of the maximum amount of energy that an organism could derive from its food if it were completely oxidized.

A heterotrophic organism must obtain sufficient chemical energy for nutrition while maintaining a thermal

balance. Moving into the warm sun to acquire heat is as much a part of the maintenance energy as obtaining the thermal energy by oxidation of carbohydrates. While the organism may modify its chemical energy requirements by changing its thermal energy environment, it may not substitute thermal for chemical energy. Unlike a Carnot heat engine, animals cannot use thermal energy to produce mechanical work. Animals depend on the chemical energy of food to accomplish work. Homeothermic animals have the ability to utilize chemical energy to supplement thermal energy to maintain their body temperature.

In any population of heterotrophs, chemical energy enters as ingested nutrients. The gross energy intake ultimately leaves the population by three different pathways: (1) waste materials egested as a by-product of either the digestion or the metabolism of the food substances, (2) production, or storage, by the organisms of substances that are yielded to a consumer organism of another species, and (3) energy lost as heat. Wiegert (1964) states that the Gibbs free energy equation, $\Delta F = \Delta H - T\Delta S$, may be used to describe energy flow through an individual, a population, or a trophic level. The energy passed to consumers in another trophic level is considered free energy (ΔF). The energy lost to the atmosphere as heat represents the sum total of the entropy gain from the several transformations which take place

within the body during the production and maintenance of the population and is unavailable for use by consumers ($T\Delta S$). Population energy utilization is stated as the sum of respiration plus production ($T\Delta S + \Delta F$) and equals the assimilation of metabolizable energy (ΔH).

Slobodkin (1962) casts considerable doubt on the direct applicability of equilibrium thermodynamics to ecological systems by pointing out that apart from other theoretical and operational difficulties, an immediate problem arises from the fact that an ecological community cannot in any sense be considered as thermodynamically isolated, nor can a system containing a living organism be considered in thermodynamic equilibrium. Slobodkin continues that the most interesting theorems of thermodynamics do not seem to apply to ecological systems in any direct way and therefore the value of translating directly measurable ecological parameters into the language of thermodynamics is not obvious. He suggests that a review of energy relations in ecology could be written with suitable incorporation of all relevant data, without mentioning either entropy or information in their rigorous meaning.

With respect to equilibrium thermodynamics, I must agree with the statement of Spanner (1964): "Thermodynamical ways of thinking represent a discipline and in this way they have a value over and above the results to

which they lead." Equilibrium thermodynamics is useful as a conceptual framework for the study of ecological systems. Current concepts in the thermodynamics of the steady state seem more applicable to ecological systems, but there still remains the necessity for making the assumption that the system is not too far from equilibrium. Hubbell (1971) notes that attempts to reduce ecology to thermodynamics have not been notably successful thus far and that the usual reason given for their lack of success is the current inadequacy of theory in steady state thermodynamics. He concludes that it is unrealistic to expect the laws of thermodynamics to explain the organization and function of biological systems, but at the same time, no correct law about biological systems may violate thermodynamic principles.

The first major interest in biological energetics had its origins in the investigations of Lavoisier in the late 18th century. Kleiber (1961) describes these and other early experiments in animal energetics. A number of studies on the energetics of individual animals have been done since the 1930's. King and Farner (1961) give an extensive discussion of energy metabolism in birds. Hart (1957, 1963, 1964) discusses the energetics of homeotherms. A collection of papers on the comparative physiology of thermoregulation is edited by Whittow (1970). Brody (1945) and Kleiber (1961) are comprehensive references

in animal energetics. Examples of primarily physiological studies of individual organisms which have been conducted in an ecological context are Pearson (1954), Pearson (1960), and West (1960). Investigations of animal energetics at the population level are illustrated by Richman (1958), Slobodkin (1960), McNab (1963), and Wiegert (1964).

Another approach to the subject of ecological energetics developed primarily from the trophic-dynamic concept of Lindeman (1942). The trophic-dynamic approach is primarily concerned with food levels, the assignment of populations to trophic levels, and an assessment of the total energy flow through the ecosystem. Examples of trophic-dynamic studies are: Teal (1957), Golley (1960), Engelmann (1961), Teal (1962), Odum, Connell, and Davenport (1962), Wiegert, Odum, and Schnell (1967), and Engelmann (1968). Concepts in studies on the secondary productivity of terrestrial ecosystems are reviewed by Petruszewicz (1967). Engelmann (1966) presents an excellent review of terrestrial field studies in animal energetics and productivity. Several authors (Margalef, 1968; Wiegert, 1970; Smith, 1970; Hubbell, 1971) have emphasized the importance of examining the rates of transfer of energy and the nature of the feedback loops between trophic levels.

The intent of this study is to determine the thermal and chemical energy fluxes of an individual predator and to use that information in estimating the energy transfer from prey populations to the predator population on a seasonal basis. The short-tailed shrew, Blarina brevicauda, was selected as the predator for a number of reasons. It is an homeotherm which is active during the entire year and thus may be exposed to extreme winter conditions. Small insectivores, such as Blarina, are known to have high metabolic rates. Winter conditions may impose additional metabolic demands because (1) energy must be used in thermoregulation and (2) the invertebrate fauna becomes less active and possibly less abundant. The relative abundance of Blarina in mature forests allows concentrated trapping efforts and larger sample sizes. Extrapolation from a single Blarina to a population is made less difficult because captured individuals appear to function identically.

Analysis of thermal radiation factors and their relationships allows calculation of the range of metabolic rates suitable for certain climatic conditions. Animal properties which affect the exchange of thermal energy are metabolic rate, moisture loss rate, conductance of fat or fur, absorptivity to radiation, and body size, shape and orientation. On a seasonal basis a Blarina could change its metabolic rate, moisture loss rate, and

conductance of fat and/or fur. On a daily basis it could change metabolic rate, body orientation, and the conductance of the fur.

Experiments examining chemical energy input and output, as well as internal mechanisms such as metabolism, behavior, and insulation were all done with respect to the thermal environment of the predator.

The prey subsystem is composed of the litter fauna, primarily ground-dwelling beetles. The composition, abundance, distribution, and energy content are characteristics of the prey which may change seasonally.

The project was designed and conducted after the experimental components approach as proposed by Holling (1966a, 1966b). The approach involves the breaking down of ecological processes into simple sub-processes, or components. Each component is examined experimentally and is represented by an equation or a set of equations. The component equations are combined to form a model of the original process.

A model of this predator-prey system will provide a view of how the internal mechanisms of the subsystems respond seasonally, as well as estimates of the energy transfers from prey to predator.

METHODS AND MATERIALS

Field Area

Field studies were conducted in a 6.47 acre (2.618 hectares) woodlot located 2.2 miles east and 1.4 miles south of Manotick, Ontario (45° 14', 75° 37'). Two edges of the woodlot are bounded by unimproved roads with adjacent wooded vegetation. The other two sides adjoin old, grassy fields. The vegetation of the woodlot is typical of mature deciduous forests in much of northeastern North America. Characteristic tree species include sugar maple (Acer saccharum), beech (Fagus grandifolia), yellow birch (Betula lutea), with smaller numbers of striped maple (Acer pennsylvanicum) and eastern hemlock (Tsuga canadensis). Large, well-decayed stumps remain from lumbering which was done several years ago. The leaf litter and humus layer is as much as 30 cm deep. The area is well-drained except along the western edge where there is standing water until early summer.

Environmental temperatures were measured using a ten-channel recording tele-thermometer. Thermistors were located in the following positions: (1) 20 cm

inside a decayed stump, (2) at the soil:leaf litter interface, and (3) on the leaf litter surface. Each location was duplicated. In the summer the dense tree canopy shaded these locations except during very brief periods at midday. A five minute record at each location was made once every two hours. Two recorder channels were used for output from a net radiometer. The net radiometer was constructed after the design of Suomi and Kuhn (1958), incorporating the modifications suggested by Moen (1969). This instrument has thin polyethylene covers which allow transmission of essentially all wavelengths of energy. The radiometer was located in the same area as the thermistors. The radiometer bottom surface was positioned at a height of 50 cm from the litter surface. No radiometer recordings were made during rainfall in the summer, or at any time in the winter. Temperatures were recorded from 12 August to 14 September, 1970 and from 24 February to 15 March, 1971.

All equipment and instruments were housed in a mobile field laboratory. No 110v AC current was available; therefore 12v DC battery-powered current inverters were used to supply AC current for electronic instruments.

Capture and Care of the Shrews

Twenty-five experimental shrews were trapped in the Manotick woodlot. Ten shrews were taken from

Algonquin Provincial Park, Ontario in March, 1970. Conventional 7.5 x 7.5 x 30 cm live traps, baited with raw hamburger, were used in all trapping. Traps were checked at least twice daily and usually more often. A total of 110 Blarina were trapped from all locations; 75 died in the trap or shortly after removal.

The shrews were kept individually in 24 x 24 x 38 cm wire cages. Each cage had a 15 cm deep layer of humus and leaf litter in the bottom. Shrews kept at cold temperatures typically made spherical leaf nests. Each shrew was fed a "shrewburger" every evening. A shrewburger is a 5 gm portion consisting of ingredients in the following proportions: 150 gm Pablum mixed cereal, 825 gm hamburger, 225 gm ground beef liver, and 600 ml V-8 vegetable juice. This combination has a caloric equivalent of 6340 ± 20 calories per gram dry weight. A typical shrewburger would contain about 10 kcal. Usually not all of the shrewburger was eaten; this remainder was removed daily. Shrewburgers were supplemented occasionally with small quantities of whole sunflower seeds. Water was provided ad lib.

Experiments were arranged to maximize the data obtained from each individual as soon after capture as possible. Most experiments were conducted within two weeks of capture. Summer-trapped shrews were kept in a controlled temperature room at 23° C with a 16:8

(day:night) light cycle. Winter-trapped shrews were kept in a 3° C room with a 10:14 (day:night) light cycle. These temperatures were selected from preliminary temperature data taken in shrew habitat. The phases of the light cycles were adjusted to simulate that appropriate seasonal conditions.

Accurate aging and sexing of Blarina requires dissection, thus this information was unavailable for live animals. For all Blarina trapped, there were never any external morphological differences observed; they appeared identical in color and size. Sexing, but not aging, was done on shrews killed during trapping and on experimental shrews after use.

Prey Sampling

Twelve pit traps, made from 21 cm top diameter, plastic flower pots were placed in the Manotick woodlot. A complete description of these pit traps is given by Barlow (1970). These pit traps were checked twice daily from 12 August to 20 August, 2 September to 14 September, 1970, and from 2 March to 14 March, 1971. Captured organisms were used in other experiments or taken as samples for bomb calorimetry.

A 2 m x 2 m sample of humus and leaf litter was taken in March, 1971. This sample was the area enclosed by the Closed Control enclosure (see Field Enclosures for details). A depth of approximately

80 cm of snow was removed, then the area was dug to bare soil, at a depth of approximately 20 cm. The humus and leaf litter was bagged and returned to the laboratory for organism removal. These organisms were used as samples for bomb calorimetry.

Field Enclosures

Three 2 m x 2 m enclosures were constructed in the Manotick woodlot. The walls were galvanized sheet metal bolted to angle-iron posts. The walls were buried in the mineral soil, leaving about 65 cm wall height above the leaf litter. Two animal enclosures were designated Experimental Pens #1 and #2, and intended as replicates. The third enclosure was designated as the Closed Control Pen. A fourth enclosure was laid out as an Open Control Pen; posts but no metal walls were installed. These four areas were selected to be as much the same as possible. All had similar types and amounts of leaf litter and each had a large, well-decayed stump within. The interior leaf litter was not disturbed by the installation of the pen walls. Small mammal traps were set in each walled pen for the first two days to insure that no small mammal had been enclosed.

Experimental Pens #1 and #2 each had thermistor probes at the litter surface, soil-litter interface, and 20 cm into the decayed stump. Each Experimental Pen also had five "activity tunnels" located in the leaf litter.

These tunnels, 4 cm inside diameter and 20 cm in length, were constructed of black plexiglas. When a shrew entered the tunnel, the floor was depressed slightly, completing an electrical circuit and sending a signal to an Esterline-Angus event recorder. Previous observations had shown that Blarina quite readily enters these tunnels.

Each pen had ten funnel pit traps. These traps were constructed by fitting a 24 mm bore plastic funnel into a 25 mm x 100 mm shell vial. The funnel top opening was 80 mm. The funnel pit traps were sunk flush with the humus layer using a soil corer. Covers of 100 mm diameter, supported on three 50 mm wire legs, were used to exclude rain and debris. These traps were checked every evening. The number of organisms of each taxon was recorded and the organisms were returned to the enclosures.

The Open Control Pen was designed to: (1) estimate the number of organisms in a 2 m x 2 m area, (2) measure the daily variability of capture success, and (3) be an unwallled comparison to the walled pens. The Closed Control Pen excluded any shrews, as well as restricting the prey to that area; thus keeping the number of prey organisms relatively stable. Captured prey organisms were returned daily to the Experimental Pens as with the Control Pens. In each Experimental Pen, the shrew depleted the food resources and the natural prey had to be supplemented. Known quantities of each

prey species were added daily, using the captured organisms from the flower pot pit traps as the supply. The Open Control Pen served as a set-point for determining the number of prey organisms to be added to each enclosure each day. If the number of captures in the Open Control Pen approximated the number of captures in the Closed Control Pen, then no new prey were put into the Closed Control Pen. When few or no prey were captured in an Experimental Pen with a shrew, then the number of prey captured in the Open Control Pen determined the number of prey to be added to each Experimental Pen.

Field enclosure experiments were conducted in August and September, 1970. A total of five Blarina were tested. The duration of an individual test ranged from one day to ten days.

Bomb Calorimetry

All samples were freeze-dried to constant weight. Weighing was done to the nearest 0.1 mg with a Mettler analytical balance. Small samples were hand-ground with a small mortar and pestle. Larger samples were ground in a Wiley mill. All samples were pelletized. Caloric equivalents were determined with a Model 1241 Parr Automatic Adiabatic Calorimeter (± 1 calorie). All standardizations and determinations were conducted according to the Parr Instrument Manual No. 142. Ash determinations were made and all caloric equivalents reported are per freeze-dried, ash-free gram.

Consumption of Natural Foods

A variety of potential prey organisms were placed in a 60 cm x 80 cm x 60 cm fiberglas box, located in a constant temperature room at 23° c. A layer of leaves about 10 cm deep was added. A shrew was put in the box for 12 hours. When the shrew was removed, the remaining prey were counted. Five summer-caught shrews were used.

A second natural food consumption test was done in the usual animal cages, but without any leaf litter. Shrewburgers were dyed with Orange I biological stain. The day before the test, the shrew was fed dyed shrew-burger, so that pre-test feces were colored. Two tests were done using Carabus nemoralis and two tests were done using Pterostichus ssp. The cage was in a 23° C constant temperature room. After 12 hours, uneaten food, food residues, dyed feces, and undyed feces were collected. No urine was collected. Four summer-caught shrews were used.

Natural food consumption on a daily basis was estimated under nearly natural summer conditions, as described in the section on Field Enclosures.

Predators's Functional Response to Changes in Prey Density

The term "functional response" as used by Holling (1959) is defined as the change in the number of prey consumed by an individual predator in response to a change in the prey density.

An environmental cabinet was programmed to

simulate the temperatures of either a mean summer day or a mean winter day, based on the temperature records taken in shrew natural habitat. Inside the cabinet was a 120 cm x 150 cm wooden box filled with about 10 cm of dead beech and maple leaves. A 30 cm x 30 cm x 30 cm stack of cardboard egg packing was provided as a nest. Water was given ad lib. Eight microswitch tunnels were used to measure locomotor activity. Only two winter-caught shrews were used in this experiment, but each animal was tested under both summer and winter conditions. A shrew was placed in the box in the evening of the first day with shrewburger as food. The next day at the same time any remaining shrewburger was removed and a known number and weight of Tenebrio larvae (mealworms) were sprinkled over the leaves. Then each succeeding day, the remaining mealworms were removed and a new supply added. Four amounts of mealworms were used: 40, 60, 80, and 100. The amount placed in the box each day was selected randomly. The total test time per individual under each environmental condition required six days.

An independent check on daily food consumption under these same experimental conditions was done by holding the food input constant by removing any remaining mealworms and adding 60 each day. Each shrew was tested for six days under each environmental condition as before.

The caloric equivalent to the mealworms was determined by bomb calorimetry to allow conversion of biomass of larvae eaten to their energy content. No attempt was made to collect the feces or urine of the shrews.

Oxygen Consumption Basic Method

All oxygen consumption experiments were based on the methods of Depocas and Hart (1957). These methods utilize the Pauling paramagnetic oxygen analyzer to measure the partial pressure of oxygen in the metabolism chamber outlet air of an open-circuit system. In two experiments, "Locomotor Activity Costs" and "Thermal Balance", oxygen consumption of the animal was calculated using the equation:

$$V_{O_2} = V_I \frac{P_{IO_2} - P_{EO_2}}{P_B - P_{EO_2}}$$

where,

V_{O_2} = the oxygen consumption of the animal per minute

V_I = the volume of air flowing into the metabolism chamber per minute

P_{IO_2} = the partial pressure of oxygen in the inlet air

P_{EO_2} = the partial pressure of oxygen in CO₂-free outlet air

P_B = the barometric pressure.

All volumes are in ml and all pressures are in mm Hg.

All oxygen consumption values are corrected to standard temperature (0° C) and pressure (760 mm Hg). A third

experiment, "Assimilation", required modifications of the basic method; these modifications are discussed later.

The oxygen analyzer was a Beckman Model C2 Paramagnetic with a range of 100 to 160 mm Hg partial pressure of oxygen and an accuracy of ± 0.5 mm Hg. Air was pumped through the system by a Neptune Model 2 Dynapump. The air was dried using Drierite and the CO₂ removed with Fisher Indicarb. Air flow rate was monitored by a Matheson Model 601 flow meter. Barometric pressure was measured with a Short and Mason Micro Barograph. The metabolism chamber was a plexiglas cylinder, 25 cm long by 10 cm diameter. The chamber had a removable, semicircular, plexiglas tray with a 5 mm mesh screen wire floor. A 40 dram, black, perforated, plastic vial was provided as "shelter" for the shrew. Some experiments required that the oxygen analysis equipment be in a controlled temperature cabinet at cold temperatures. In such cases, a foam-insulated, glass-fronted box with heating coils and a blower was used to maintain the appropriate ambient temperature for the equipment.

Assimilation

The oxygen consumption equipment described earlier was used, but with additional instrumentation and alteration of the method. As this experiment was designed to run for eight hours, standardization of

air composition, pressure, and flow rate was desirable. A Linde pure air mixture containing 20.00% O₂ was put into the system using a dual stage regulator. A slight suction was provided on the opposite end of the system by using the vacuum coupling of the Dynapump. Pressure was monitored with a 300 mm mercury manometer. By adjusting the gas regulator and two precision needle valves, a standard pressure of 760 mm Hg (159 mm Hg partial pressure of O₂) and an air flow rate of 150 cc/min could be maintained. As the Beckman paramagnetic oxygen analyzer has no recorder output, a Beckman Model 777 Polarographic Oxygen Analyzer was used to constantly monitor the O₂ partial pressure of the metabolism chamber outlet air flow. The polarographic analyzer output was recorded on a Leeds and Northrup potentiometric chart recorder. The accuracy of this recorded data was ± 1 mm Hg. Oxygen partial pressures of inlet and outlet air were checked visually at frequent intervals with the more accurate (± 0.5 mm Hg) Beckman paramagnetic analyzer. The total volume of CO₂ produced was measured gravimetrically by passing the dried outlet air through gas analysis bottles containing Fisher Indicarb as the CO₂ absorbent. The total O₂ consumption was measured from the summation of the per minute consumption rates over the entire period (480 minutes). The per minute consumption was calculated from the equation:

$$V_{O_2} = V_E \frac{P_{IO_2} - P_{EO_2}}{P_B - P_{IO_2}}$$

where, V_{O_2} = the oxygen consumption of the animal per minute

P_{IO_2} = the partial pressure of oxygen in the inlet air

P_{EO_2} = the partial pressure of oxygen in the CO_2 -free outlet air

P_B = the barometric pressure

V_E = the volume of CO_2 -free outlet air per minute.

To minimize fluctuations around the desired temperature in the metabolism chamber, the chamber was submerged in a $\pm 0.1^\circ C$ constant temperature water bath. The inlet airstream was adjusted to the selected temperature by passing it through a long, submerged coil just before the air entered the metabolism chamber. The temperature of the air in the metabolism chamber was recorded throughout the duration of the test with a single channel tele-thermometer.

At the beginning of a test, a known weight of shrewburger, dyed with Orange I biological stain, was placed in the chamber. The semicircular tray was partially filled with mineral oil. A second screen (1 mm mesh) was placed under the 5 mm mesh screen floor. This arrangement allowed feces to drop through the first screen onto the second screen where they were retained. Urine passed through the second screen and into the mineral oil, used to prevent evaporation of the urine.

The shrew was provided with a 40 dram, perforated, black plastic vial as "shelter". All experiments were begun at approximately 1400 hours. A 15 minute equilibration period was allowed before beginning to record. At the end of the 8 hour period, the shrew, remaining food, dyed feces, undyed feces, and urine were collected and weighed. Determination of caloric equivalents was done for the food, feces, and urine.

The experimental design was a 2 x 2 factorial analysis of variance. One factor was the season of capture of the shrew. The second factor was the test temperature. Nine summer-caught shrews were tested at 3° C and 23° C and nine winter-caught shrews were tested at 3° C and 23° C.

Locomotor Activity Costs

The basic oxygen consumption method was used. The equipment was located in a constant temperature room. After a shrew was placed in the metabolism chamber, there was an interval of 30 minutes before observations were started. Locomotor activity was divided subjectively into four levels: (1) deep sleep, (2) interrupted sleep, (3) normally active, and (4) hyperactive. The following data were recorded at five minute intervals: (1) characteristic activity level, (2) partial pressure of O₂ in the outlet air, (3) air flow rate, and (4) metabolism chamber air temperature. Forty such obser-

vations were made during a period of three hours and fifteen minutes. The experiment had three test conditions: (1) summer-caught shrews tested at 23° C, (2) fall-caught shrews tested at 15° C, and (3) winter-caught shrews tested at 3° C. Under each condition, 200 observations were made on five shrews.

Thermal Balance

The basic oxygen consumption method was used. The metabolism chamber had an extendable, 5 mm diameter, rod mounted in a gas-tight, ball-joint fitting at one end of the chamber. A Yellow Springs Instruments small surface thermistor (time constant 0.3 seconds) was mounted on the tip of the rod. This thermistor could be positioned quickly anywhere inside the metabolism chamber. With this arrangement, the temperature at the fur surface at a central dorsal location could be measured without disturbing the shrew. A YSI air temperature thermistor monitored the metabolism chamber air. Temperatures were measured and read to the nearest tenth of a degree with a YSI Model 46 TUC tele-thermometer. Wind speed was measured by a Weather Measure Corporation Model W141-a hot wire anemometer. At an air flow rate of 150 cc/min, the wind speed in the metabolism chamber at the screen floor level was 20 ± 2 cm/sec. Thermal radiation at each observation time was measured by the net radiometer described under "Field Area". The shrew

was placed in the metabolism chamber on the screen floor with no plastic vial or food. The entire apparatus was placed in a programmable environmental cabinet. The initial cabinet temperature was 28° C. This temperature was held for 15 minutes for the shrew to become accustomed to the metabolism chamber and for the oxygen analysis equipment to be adjusted. Then the environmental cabinet started a decreasing linear temperature ramp. The temperature decreased in the metabolism chamber approximately 1° C per 5 minutes. This decrease continued until -8° C was reached after about three hours. At five minute intervals the following data were recorded: (1) partial pressure of O₂ in the outlet air, (2) the temperature at the fur surface of the shrew, (3) the metabolism chamber air temperature, (4) the net radiation flux, (5) the locomotor activity level of the shrew, and (6) the postural behavior of the shrew. Postural behavior is the position in which the animal sits when normal locomotor activity ceases. The postures were referred to as: (1) spherical, (2) normal sitting, and (3) spread. At 30 minute intervals the partial pressure of the O₂ in the inlet air, the air flow rate, and the barometric pressure were recorded. Eight summer-caught and eight winter-caught shrews were used in this experiment.

Carcass Cooling

When dead shrews were found in the small mammal traps, they were returned to the laboratory and frozen. Ten of these shrews were selected per trapping season (summer, fall, and winter) for the carcass cooling experiment. Individuals were selected only if their fur was in a natural condition, not matted, flattened, or dirty. A dead shrew was placed in a warm oven and slowly heated to an internal body temperature of 40° C. A YSI small animal rectal probe was inserted in the anus to a depth of 30 mm. The shrew was placed on a screen floor in a natural sitting position. A YSI air temperature probe was mounted within 5 cm to monitor ambient temperature. This unit was placed in a constant temperature cabinet at 3° C. A polyfoam box was placed over the unit to eliminate small air currents and any radiation from the cabinet lighting. The polyfoam box also helped to stabilize the ambient temperature, such that fluctuations were $\pm 0.2^{\circ}$ C. Two YSI Model 46 TUC tele-thermometers and two Cole-Parmer Mark VII recorders were used to monitor the changes in the ambient air temperature and body core temperatures during a 60 minute cooling period.

Statistical and Computer Techniques

Statistical tests were taken from Steel and Torrie (1960), Dixon and Massey (1957), and Quenouille (1966). Measures of variability reported as $\pm$ indicate the 95% confidence limits. In most cases variance is indicated by reporting the standard deviation (SD). All linear regressions were done using the least-squares technique. Goodness-of-fit was tested by F values. When space permits, the 95% confidence limits of regression lines are presented graphically. Comparisons of two regression lines, testing differences in slope and intercept, were done as suggested by Quenouille (1966).

All statistical analyses were done on the Carleton University XDS Sigma 7 digital computer. Both Basic and Fortran IV programming languages were used. Simulation techniques for the model were done in Fortran IV on the Sigma 7.

RESULTS

Thermal Environment

August

Hourly, as well as daily, fluctuations were the greatest on the leaf litter surface (Fig. 1). The mean nightly low is 14.2°C ; the mean daily high is 26.2°C . Variances about the mean include the differences in the two locations as well as daily differences. The widest range of temperatures at any given time is 12°C . The daily temperature pattern is best represented by the mean temperatures. The 95% confidence limits give an indication of daily mean fluctuations, the greatest being $\pm 4^{\circ}\text{C}$. The temperature at the soil-litter interface is moderated by the leaves (Fig. 2). The mean nightly low is 16.8°C and the mean daily high is only 21°C . The widest range of temperatures at any given time is 8°C . The greatest daily mean fluctuations are $\pm 2^{\circ}\text{C}$. Inside the soft, well-decayed wood of the rotted stump, hourly variation is very small (Fig. 3). The mean nightly low is 17°C and the mean daily high is 18°C . The widest range of temperatures at any given time is 5°C . The greatest daily mean fluctuations are $\pm 1^{\circ}\text{C}$.

FIG. 1. Temperatures measured at the leaf litter surface in the Manotick woodlot during 12-20 August 1970. Vertical bars indicate the 95% confidence limits. Numbers by the means are sample sizes. Open circles indicate the ranges. Two locations were measured at each time interval.

FIG. 2. Temperatures measured at the soil-leaf litter interface in the Manotick woodland during 12-20 August 1970. Vertical bars indicate the 95% confidence limits. Numbers by the means are sample sizes. Open circles indicate the ranges. Two locations were measured at each time interval.

FIG. 3. Temperatures measured 20 cm inside decayed stumps in the Manotick woodlot during 12-20 August 1970. Vertical bars indicate the 95% confidence limits. Numbers by the means are sample sizes. Open circles indicate the ranges. Two locations were measured at each time interval.

Incoming radiation (Fig. 4) is greatest between 1200 and 1400 hours, a time when some direct sunlight can fall on the forest floor. The mean daily maximum temperature at the leaf litter surface occurs during this mean maximum insolation of $0.641 \text{ cal/cm}^2/\text{min}$. The wide range and 95% confidence limits about the mean maximum insolation indicate variation among bright and cloudy days. The variation in cloud cover is less obvious at other times of day as the shade created by the tree canopy masks this difference. Terrestrial radiation also is greatest between 1200 and 1400 hours (Fig. 5). The mean maximum terrestrial radiation is $0.536 \text{ cal/cm}^2/\text{min}$. The highest incoming mean net radiation ($0.116 \text{ cal/cm}^2/\text{min}$) occurs at this time. The highest outgoing mean net radiation ($0.025 \text{ cal/cm}^2/\text{min}$) occurs from 0600 to 0800 hours.

March

The insulative effect of approximately 80 cm of snow eliminated temperature fluctuation. The temperature was 0° C and there were no differences in the temperatures of the three locations at a given time, nor was there any difference in hourly or daily temperatures in any location.

FIG. 4. Incoming radiation at 45 cm from the litter surface in the Manotick woodlot during 12-20 August 1970. Vertical bars indicate the 95% confidence limits. Numbers by the means are sample sizes. Open circles indicate the ranges.

FIG. 5. Terrestrial radiation at 45 cm from the litter surface in the Manotick woodlot during 12-20 August 1970. Vertical bars indicate the 95% confidence limits. Numbers by the means are sample sizes. Open circles indicate the ranges.

Shrew Population

Ninety-six dead shrews, trapped from several locations over a two year period, were sexed: 45 were females and 51 were males, a ratio of 1.16 males per female. Four of these females were pregnant; one was trapped in March, one in May, and two in July. Males with enlarged testes were trapped in February, March, July, September, and November. Ages of these shrews were not determined. During the two year period, 78 shrews were trapped in approximately 6000 trap nights in the Manotick woodlot alone. Using the same number of traps, shrews were more frequently trapped in the summer than in the winter. This may not represent a change in shrew abundance, since winter trapping procedures were far more difficult and additional effort was required to keep the traps operational.

Productivity, as defined by Golley (1967), is the rate of increase of organic matter or energy through tissue growth and/or new individuals entering a population. Measures of individual energy flow in the present project did not include a measure of productivity because all shrews were adults and no reproduction occurred.

Pearson (1945) estimated a Blarina population to have a 20% mortality each month. Over a period of six months an initial population of 100 shrews would lose 74 individuals at that rate. To remain stable the

population must maintain equal mortality and natality. Assuming that all individuals in the original population are adults, productivity may be estimated. If 74 adults die in a six month period, then 74 individuals must be born and grow to maturity in that period in order to maintain the population. A 20 gm, adult Blarina has an energy content of 35.25 kcal (Appendix I). The 74 adults represent about 2609 kcal of production in six months or 145 cal/individual/day.

Prey Sampling

In both summer and winter sampling procedures, organisms which were less than 2 mm in length or which occurred very rarely were excluded. The remainder of the invertebrate ground-dwelling forest fauna are referred to as the potential prey.

Summer

Preliminary quadrat sampling and pit trapping indicated that pit trapping was a better method for estimating prey availability in the summer. The litter arthropods are very active at warm temperatures. This activity increases the effectiveness of pit traps, but decreases the accuracy of quadrat sampling, since many arthropods escape easily during sampling procedures. Except for a few spiders, all of the potential prey were caught during the night. Caloric equivalents were determined by bomb calorimetry (Appendix I). These

captures are given in units of kilocalories per night for the twelve flower pot pit traps (Table 1). The mean total capture in August was 6.232 kcal/night. The captures from the ten funnel pit traps in the Open Control enclosure are given in Table 2. The mean total capture for August was 1.510 kcal/night. A large proportion of the energy value for August is from Carabus; due both to its large size and high activity at this time of year.

With cooler nights in September, litter arthropod activity slowed and the pit traps were less effective. The mean total capture of the flower pot pit traps was 1.724 kcal/night (Table 1). The mean total capture of the funnel pit traps was 0.467 cal/night (Table 2). No Carabus were caught from 2 through 14 September.

As temperature data were available for these trapping periods, an attempt was made to express litter arthropod activity as a function of leaf litter temperature. No meaningful relationship was found. When the mean nightly litter surface temperature was below 14° C no Carabus were captured.

Sample sizes, dry weights, and caloric equivalents for each taxon are in Appendix I.

Winter

The pit traps caught only a few spiders during the entire winter trapping period. Assessment of the "standing crop" rather than litter arthropod activity,

TABLE 1
ENERGY CONTENT OF FLOWER POT PIT TRAP CAPTURES

Organism	kcal/night for			
	8-20 $\bar{x}$	August SD	2-14 $\bar{x}$	September SD
<u>Carabus</u>	2.943	2.071	0	
<u>Pterostichus</u>	1.088	0.449	0.851	0.518
<u>Calathus</u>	0.099	0.085	0.104	0.104
<u>Ceuthophilus</u>	1.829	1.313	0.553	0.444
Julida	0.109	0.092	0.064	0.053
Lycosidae	0.113	0.106	0.119	0.119
Other spiders	0.051	0.037	0.033	0.030
Σ	6.232	4.153	1.724	1.268

TABLE 2
ENERGY CONTENT OF FUNNEL PIT TRAP CAPTURES

Organism	kcal/night for			
	8-20 $\bar{x}$	August SD	2-14 $\bar{x}$	September SD
<u>Carabus</u>	0.318	0.332	0	
<u>Pterostichus</u>	0.076	0.075	0.042	0.043
<u>Calathus</u>	0.067	0.120	0.022	0.040
<u>Ceuthophilus</u>	0.686	0.534	0.342	0.441
Julida:	0.033	0.031	0.026	0.029
Lycosidae	0.096	0.111	0.053	0.086
Other spiders	0.173	0.126	0.024	0.032
Annelida	0.061	0.162	0	
Σ	1.510	1.491	0.467	0.671

TABLE 3
ENERGY CONTENT OF PREY FROM CONTROL ENCLOSURE

Organism	kcal/4 m ²
<u>Acrosternum</u>	6.945
<u>Vespula</u>	0.891
<u>Mesodon</u>	2.641
Julida	3.399
Lycosidae	1.178
Henicopidae	0.989
Elateridae larvae	4.855
Tipulidae larvae	2.692
Lepidoptera larvae	0.282
Carabidae larvae	0.541
Noctuidae pupae	1.317
Annelida	7.744
Σ	33.473

then was a better estimate of prey availability. Since the 2 m x 2 m winter sample was taken from the Closed Control enclosure, it represents an undisturbed potential prey resource. The enclosure walls prevented any foraging by resident shrews. Most of the potential prey were picked from the humus; few occurred in the undecomposed leaves or in the decayed wood of the stump. This sample contained 33.473 kcal per four square meters or 8.367 kcal/m². The energy content of these captures are listed by taxon in Table 3.

Sample sizes, dry weights, and caloric equivalents for each taxon are in Appendix II.

Prey Consumption

Natural Foods in Laboratory

To determine food preference, the following organisms were offered together as potential prey: Carabus, Pterostichus, Calathus, Ceuthophilus, Polydesmus, Julus, and lycosid spiders. With all five shrews tested all of these organisms were eaten, none were refused. The mean natural food consumption was 4.493 kcal/12 hr (SD = 0.079). Since all of the prey were eaten in the 12 hour period in all replicates, this mean food consumption is a minimum estimate.

In the second natural foods consumption test, food types were restricted to a single genus for each replicate. Two tests were done using Carabus and two

with Pterostichus. In all tests the shrews left chitinous body parts, such as elytra and appendages, uneaten. These uneaten parts are referred to as food residue. No soft body parts or whole beetles ever remained after the 12 hour duration of the tests. When eating 10 Carabus (5.031 kcal) the shrews left a food residue (average total energy content of 2.788 kcal), which averaged 40.78% of the total food originally available. When eating 25 of the smaller Pterostichus (5.031 kcal) the shrews left a food residue (average total energy content of 0.648 kcal), which averaged 12.90% of the total food originally available. The mean food consumption of the four tests is 4.212 kcal/12 hr (SD = 0.303). There was no difference in the shrews' average food consumption between the two food types. As with the mixed prey natural food consumption tests, this mean food consumption is a minimum estimate. There was no difference between the average energy loss in the shrews' feces. The mean energy loss in the feces is 0.764 kcal/12 hr (SD = 0.161). Digestive efficiency is calculated as $\frac{E - L}{E}$, where E is the energy content of the food ingested and L is the energy content of the feces egested; all values are in calories. The mean digestive efficiency is 81.66% (SD = 4.77). The total energy content of the 10 Carabus is greater than the total energy content of the 25 Pterostichus, but the shrews ingested and digested an equal amount of energy from both.

Natural Foods in Field Enclosures

Table 4 gives the differences between the energy content of the prey added and the energy content of the prey recaptured for each of the field enclosures. High values indicate large numbers of prey which were never recaptured; presumably eaten by the shrew. The effect of the shrew is easily seen in the total energy exchange in Enclosure #2. During the 16 days when a shrew was present, 42.917 kcal of prey were not recaptured, while during the 10 days when no shrew was present only 1.310 kcal of prey were not recaptured. An estimate of the accuracy of the technique is seen by comparing the total energy exchange of Enclosure #1 without a shrew, Enclosure #2 without a shrew, and the Closed Control. In each case less than 2 kcal of prey were not recaptured. The Open Control has a higher total energy exchange, since prey mobility was not restricted by the pen walls. However the Open Control value of 3.880 kcal is far below the values for experimental enclosures with shrews present. The majority of the total energy exchange is from Carabus, Pterostichus, and Ceuthophilus in all cases.

The daily energy exchange may be used as an index of daily food consumption of a shrew. Daily food consumption is approximately equal in Experimental Enclosure #1 and Experimental Enclosure #2, 2.813 and 2.682 kcal, respectively.

TABLE 4
ENERGY EXCHANGE IN FIELD ENCLOSURES

Organism	Encl. #1 No shrew	Encl. #1 Shrew	Encl. #2 No shrew	Encl. #2 Shrew	Open Control	Closed Control
<u>Carabus</u>	0	7.578	0	10.104	1.895	1.263
<u>Pterostichus</u>	1.265	4.427	0.316	12.016	0.632	0
<u>Calathus</u>	0.358	1.073	0	1.967	0	0
<u>Ceuthophilus</u>	0	2.743	0.457	10.058	1.372	0
<u>Julida</u>	0.168	0.252	0.168	5.671	-0.028	0.168
<u>Polydesmida</u>	0	0	0.030	0.075	0.015	-0.015
<u>Lycosidae</u>	0.128	0.640	0	1.152	0	0
<u>Other Araneae</u>	-0.052	0.167	-0.198	0.800	0	-0.052
<u>Annelida</u>	0	0	0.537	1.074	0	0
Σ kcal	1.867	16.880	1.310	42.917	3.880	1.364
# days	20	6	10	16	26	26
kcal/day	0.093	2.813	0.131	2.682	0.149	0.052

*Energy exchange is the energy content of prey captured plus any prey added to the enclosure on day n minus the prey captured on day n+1.

Predator's Functional Response
to Changes in Prey Density

Since standardized numbers, but not standardized weights of Tenebrio larvae were used as prey, the results are presented in Figure 6 as the number eaten as a function of the number available, and in Figure 7 as the kilocalories eaten as a function of the kilocalories available. The F-ratios for testing goodness-of-fit show that these data are fairly well represented by the linear regressions (Figs. 6 & 7). The lack of a significant difference in the slopes indicates that the shrews are responding in the same manner to the prey regardless of the temperature regimes. The difference in the intercepts indicates the level at which the shrew is operating. For example, if 60 larvae were available, the shrew under winter conditions is predicted to eat 57 ± 5 larvae (95% confidence limits), whereas the shrew under summer conditions, only 42 ± 6 . Since conversion of numbers of larvae to kilocalories of larvae does not change the slope of the regression lines noticeably, the same type of situation holds true. That is, for 15 kcal of larvae available, the shrew under winter conditions is predicted to eat 13.8 ± 1.2 kcal/day; the shrew under summer conditions is predicted to eat 10.2 ± 2.2 kcal/day.

When this experiment was done with the number of available larvae held constant at 60, the numbers of larvae eaten were slightly lower than the predicted

FIG. 6. Number of larvae eaten by a Blarina as a function of the number of larvae available. The dashed regression line and open circles indicate shrews tested under summer temperature conditions. The solid regression line and darkened circles indicate shrews tested under winter temperature conditions. The 95% confidence limits are indicated by the vertical bars.

Statistic	Condition	
	Summer	Winter
Regression Equation	$Y=51.63+.848(X-70)$	$Y=65.25+.815(X-70)$
No Obs	8	8
Std Error Estimate	6.986	5.394
Std Dev Slope	0.110	0.085
F-ratio Slope	58.86	91.30
Probability of significant difference in slope	ns	
Probability of significant difference in intercept	$P<.01$

FIG. 7. Kilocalories of larvae eaten by a Blarina as a function of the kilocalories of larvae available. The dashed regression line and open circles indicate shrews tested under summer temperature conditions. The solid regression line and darkened circles indicate shrews tested under winter temperature conditions. The 95% confidence limits are indicated by the vertical bars.

Statistic	Condition	
	Summer	Winter
Regression Equation	$Y=14.53+.930(X-19.55)$	$Y=14.93+.772(X-16.35)$
No Obs	8	8
Std Error Estimate	2.103	0.962
Std Dev Slope	0.117	0.045
F-ratio Slope	63.32	290.56
Probability of significant difference in slope	ns	
Probability of significant difference in intercept	$P<.05$

values from the previous variable prey availability tests. The shrews under summer conditions ate 38 ± 12 larvae per day; the shrews under winter conditions ate 38 ± 15 larvae per day. No significant difference in feeding response can be demonstrated in these results. The wide 95% confidence limits around the means of daily food consumption are best explained as being due to small sample sizes; only two winter-caught shrews were tested in each of the four experimental situations.

Conversion of numbers of larvae to the energy content of the larvae gives a mean daily food consumption of 9.35 ± 4.95 kcal for a shrew under winter conditions and a mean daily food consumption of 8.37 ± 4.15 kcal for a shrew under summer conditions. For a constant number of available larvae, shrews under winter conditions did not demonstrate a significantly different mean energy intake than shrews under summer conditions.

For the experiments employing both constant and variable numbers of larvae available, the larvae were sprinkled evenly over the leaf surface of the box. In all cases the shrew would collect these larvae and store them in the egg carton nest.

Metabolism and Assimilation

The Respiratory Quotient (Table 5) was calculated as the total volume of CO₂ produced divided by the total volume of O₂ consumed. For an animal eating a mixed diet an RQ of between .70 and 1.00 would be expected. The mean RQ for the winter-caught shrews (.84) is slightly lower than for the summer-caught shrews (.87), but these are not significantly different. The thermal equivalent of oxygen was calculated from the equation: kcal/liter of O₂ = 3.815 + 1.232 (RQ), (King and Farner, 1961). Total metabolism is expressed as kcal/8 hrs for each of the 18 shrews, using each individual's own oxygen consumption data, RQ, and body weight.

There are differences in the total metabolism in the four tests and the standard deviation is small for every mean (Table 5). Both summer and winter-caught shrews tested at 20° C have lower total metabolism means than the same shrews tested at 3° C. The 2 x 2 factorial analysis of variance for the total metabolism data (Table 6) shows a highly significant difference ($p < .001$) in metabolism at the different test temperatures. For both summer and winter-caught shrews exposure to 3° C caused an approximate doubling of the total metabolism at 20° C. Table 6 also shows a significant difference ($p < .05$) in the total metabolism between the seasons when the shrews were captured. For both 3° and 20° C the winter-caught shrews had a slightly lower mean metabolism.

TABLE 5
SUMMARY OF ASSIMILATION EXPERIMENT

Variable		Season of Capture ^a			
		Summer	Summer	Winter	Winter
		20°C	Ambient Temperature 3°C	20°C	3°C
$\bar{x}$ O ₂ ^b (cc/gm/hr)	$\bar{x}$	4.85	8.33	4.51	8.76
	SD	0.55	1.02	0.52	0.87
Respiratory Quotient		0.87 0.02	0.87 0.03	0.84 0.02	0.84 0.03
Metabolism ^c (kcal/8hr)		4.323 0.625	7.652 0.573	3.745 0.532	7.062 0.956
Food Eaten (kcal/8hr)		7.643 2.305	6.742 3.249	6.531 3.072	10.047 3.976
Feces (kcal/8hr)		1.168 0.399	1.052 0.645	0.601 0.306	1.309 0.725
Urine (kcal/8hr)		0.810 0.455	0.448 0.406	0.383 0.272	0.634 0.461
Digestive Efficiency		0.84 0.04	0.85 0.05	0.88 0.03	0.91 0.03
Digestible Energy (kcal/8hr)		6.475 2.109	5.680 2.705	5.931 2.835	8.738 3.257
Metabolizable Energy (kcal/8hr)		5.665 1.884	5.242 2.394	5.547 2.687	8.114 2.935
Energy Balance ^d (kcal/8hr)		7.342 1.460	3.590 2.184	7.135 1.779	7.053 2.619

^a Nine shrews were captured and tested each season; each individual at both ambient temperatures.

^b The term $\bar{x}$ O₂ refers to a mean of means. Oxygen consumption was measured every minute for the entire 480 minutes of a single test. The mean O₂ consumption for each shrew was calculated, then these nine means were used for calculations for each test condition.

^c Metabolism was calculated for each individual shrew using its own O₂ consumption, RQ, and body weight.

^d Mean values are coded +6.

TABLE 6
ANALYSES OF VARIANCE OF ASSIMILATION EXPERIMENT

Source	df	SS(x10 ³)	MS(x10 ³)	F	P
A. Metabolism					
Season	1	3132.90	3132.90	6.59	<.05
Temp	1	99002.50	99002.50	208.27	<.001
ST	1	1.23	1.23	.01	
Error	32	15211.79	475.37		
Total	35	117348.42			
B. Food Eaten					
Season	1	10834.00	10834.00	1.05	
Temp	1	15375.50	15375.50	1.50	
ST	1	43897.30	43897.30	4.27	<.05
Error	32	328973.00	10280.40		
Total	35	399079.80			
C. Feces					
Season	1	216.23	216.23	0.72	
Temp	1	788.54	788.54	2.64	
ST	1	1527.70	1527.70	5.12	<.05
Error	32	9549.92	298.44		
Total	35	12082.39			
D. Urine					
Season	1	129.12	129.12	0.78	
Temp	1	27.56	27.56	0.17	
ST	1	847.01	847.01	5.15	<.05
Error	32	5265.02	164.53		
Total	35	6268.71			

TABLE 6 (cont'd.)
ANALYSES OF VARIANCE OF ASSIMILATION EXPERIMENT

Source	df	SS	MS	F	P
E. Digestive Efficiency					
Season	1	0.0225	0.0225	14.77	<.001
Temp	1	0.0013	0.0013	0.88	
ST	1	0.0028	0.0028	1.87	
Error	32	0.0487	0.0015		
Total	35	0.0753			
F. Energy Balance					
Season	1	23.85	23.85	4.96	<.05
Temp	1	33.07	33.07	6.88	<.05
ST	1	30.29	30.29	6.30	<.05
Error	32	153.84	4.81		
Total	35	241.05			

Table 5 shows that for three conditions the mean food energy eaten was about 7 kcal/animal/8 hrs. For winter-caught shrews tested at 3° C, the mean food energy eaten was 10 kcal/animal/8 hrs. In all cases there is a large variance about the mean. The analysis of variance for the food eaten (Table 6) shows a significant difference ($P < .05$) for only the S x T interaction.

Table 5 shows a loss of about 1 kcal/animal/8 hrs in feces. The analysis of variance (Table 6) shows a significant difference ($P < .05$) in the S x T interaction. The energy loss in the feces is in the same approximate proportions to the energy eaten in food: (1) summer at 20°: .15, (2) summer at 3°: .15, (3) winter at 20°: .09, and (4) winter at 3°: .13.

The mean energy loss of urine is lowest at 0.383 kcal/animal/8 hrs for winter-caught shrews tested at 20° C and highest at 0.810 kcal/animal/8 hrs for summer-caught shrews tested at 20° C (Table 5). The variance in each case is high. The analysis of variance for energy loss of urine (Table 6) again shows a significant difference ($P < .05$) for the S x T interaction.

Digestive efficiency is defined as

$$\frac{\text{energy of food eaten} - \text{energy of feces}}{\text{energy of food eaten}} .$$

Table 5 indicates that winter-caught shrews had a higher digestive efficiency than summer-caught shrews.

The analysis of variance (Table 6) shows a highly significant difference ($P < .001$) in digestive efficiency. The test temperature does not affect the digestive efficiency. These data indicate that winter-caught shrews digest a slightly higher proportion of their food than do summer-caught shrews.

The energy of food eaten less the metabolic energy expended, less the fecal energy, less the urinary energy is the energy balance. A positive energy balance indicates energy available for the production of new protoplasm, either in growth or reproduction. For summer-caught shrews tested at 3° C the mean energy balance is a negative 2.410 kcal/8hrs. Even the upper 95% confidence limit does not show a positive mean energy balance. In the three other cases the mean energy balance is positive. The lower 95% confidence limits show small negative mean energy balances for each of these cases. Individual energy balances were coded (+6.0) to give all positive values and an analysis of variance was done (Table 6). A significant difference ($P < .05$) exists between seasons of capture (S), test temperatures (T), and for the S x T interaction. The main effect of season of capture (S) without respect to test temperature (T) is 1.962 kcal. The main effect of test temperature (T) without respect to season of capture (S) is 2.251 kcal. The S x T interaction effect is 1.501 kcal. With a significant interaction,

the factors are not independent of one another; the simple effects of a factor differ and the magnitude of any simple effect depends upon the level of the other factor. These statistics indicate that the primary influence on energy balance is the test temperature. However the season of capture of the shrew also influences the energy balance. Summer-caught shrews tested at 3° C had the lowest mean energy balance; winter-caught shrews tested at 20° C had the highest. The interaction effect appears to be due to the acclimatization of the shrews.

Locomotor Activity Costs

In the Assimilation experiment, only total metabolic energy was considered. In this experiment, the oxygen consumption data were used as a measure of locomotor activity costs under three different conditions (Table 7). Using Student's t-test, the mean oxygen consumption rates for all activity levels within a season are significantly different ($P < .05$) except between levels 3 and 4 for winter-caught shrews ($P < .10$). The rates for all three seasons within an activity level are significantly different ($P < .05$) except activity level 3 between summer and fall-caught shrews ($P < .10$) and activity level 4 between summer and fall-caught shrews (ns).

Assuming a 20 gm shrew with an RQ of .85, the oxygen consumption data were converted to the metabolic energy equivalents (Table 7). A linear regression of

TABLE 7
LOCOMOTOR ACTIVITY COSTS

Activity Level (AL)	Season of Capture					
	Summer		Fall		Winter	
	23°C		15°C		3°C	
	O ₂ ^a	M ^b	O ₂	M	O ₂	M
All AL						
$\bar{x}$	5.14	500	5.64	548	7.55	734
SD	1.78	173	1.43	139	1.74	169
n	200		200		200	
AL 1						
$\bar{x}$	3.58	348	4.24	412	6.01	584
SD	1.11	108	0.53	51	0.90	87
n	52		50		58	
AL 2						
$\bar{x}$	4.74	461	5.18	503	7.49	728
SD	1.41	137	0.76	74	1.43	139
n	73		71		65	
AL 3						
$\bar{x}$	6.25	608	6.58	640	8.56	832
SD	1.00	97	0.88	86	1.56	152
n	51		55		45	
AL 4						
$\bar{x}$	7.41	720	7.78	756	9.14	888
SD	1.48	144	1.30	126	1.33	129
n	24		24		31	

^a Units are cc O₂/gm/hr.

^b Metabolism is for a 20 gm, 70 cm² shrew with an RQ of .85; units are calories/animal/hour.

FIG. 8. Metabolism as a function of locomotor activity level. Details about the activity level units are in the text. Metabolism units are calories/animal/hour for a 20 gm, 70 cm² shrew with an RQ of .85. The 95% confidence limits are indicated for each regression line. The lines are for shrews trapped in summer (long dash), fall (short dash), and winter (solid).

Statistic	Condition		
	Season of Capture		
	Summer	Fall	Winter
	Ambient Temperature 23°C	Ambient Temperature 15°C	Ambient Temperature 3°C
Regression Equation	$Y=534.25-126.30(X-2.5)$	$Y=577.75-116.90(X-2.5)$	$Y=758.00-101.6(X-2.5)$
No Obs	200	200	200
Std Error Estimate	10.916	13.797	31.138
Std Dev Slope	4.882	6.170	13.925
F-ratio Slope	669.40	358.96	53.23

Probabilities of significant differences in slope:

Summer-Fall ns	Summer-Winter ns	Winter-Fall ns
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Probabilities of significant differences in intercept:

Summer-Fall P<.05	Summer-Winter P<.001	Winter-Fall P<.001
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metabolism on the observed locomotor activity levels (AL) was done for each seasonal condition. These regression lines are presented in Figure 8. There is no significant difference in the slopes of the lines. The intercepts of these lines are all significantly different (Figure 8). For a one unit increase in activity level under any of these conditions, metabolism increased by approximately 100 cal/animal/hr. When compared to a summer-caught shrew at 23° C, a winter-caught shrew at 3° C uses 236 cal/hr more for thermoregulation during deep sleep (AL 1) and 224 cal/hr more for thermoregulation during normal exploring activity (AL 3).

Activity Distribution

Activity distribution was monitored during the predator's functional response to prey density experiments done in the programmed environmental chamber and during the natural foods consumption experiments done in the field enclosures. Figure 9 shows the patterns for the four conditions under which the functional response experiment was conducted. The shrews used in this experiment were all winter-caught. Under the summer temperature regime there is no difference in activity distribution between constant and variable food supply. Under the winter temperature regime shrews with a variable food supply show the same distribution but a greater intensity of activity in the early morning hours than

FIG. 9. Daily activity patterns of Blarina. High numbers of microswitch tunnel marks indicate high locomotor activity. All patterns shown are from experiments of 12 days duration.

Pattern	Experiment Location	Weather Conditions	Food Input
a	Environ. Cabinet	Winter	Variable
b	Environ. Cabinet	Winter	Constant
c	Environ. Cabinet	Summer	Variable
d	Environ. Cabinet	Summer	Constant
e	Field Enclosure	Summer	Variable

shrews with a constant food supply. Figure 9 also shows the activity distribution of shrews in the field enclosures. The daily activity pattern in the field is very similar to that found under laboratory conditions. The field enclosure had many natural "tunnels" in the leaf litter and decayed stump, whereas in the box used in the environmental cabinet, nothing but the egg carton nest and microswitch tunnels was provided. The box had an area of 1.8 m^2 , but the field enclosure had an area of 4.0 m^2 . Since eight microswitch tunnels were used in each case, there was a lower chance of a shrew entering a microswitch tunnel in the field enclosure.

Typically activity is high between 1800 and 0600 hours and very low between 0700 and 1700 hours. Under the conditions tested, activity was distributed in a somewhat bimodal pattern in time (Figure 9).

Thermal Balance

Regressions of oxygen consumption on ambient temperature are in Figure 10 for activity level 2 and in Figure 11 for activity level 3. For both activity levels, the summer-caught shrews have a significantly higher oxygen consumption rate. Assuming a 20 gm shrew with an RQ of .85, these oxygen consumption data were converted to metabolic energy. Metabolism as a function of ambient temperature, both for two specific activity levels and including all activity levels, is in Figure 12.

FIG. 10 a. Oxygen consumption in cc/gm/hr of summer-caught shrews while exhibiting activity level 2 (interrupted sleep) in the Thermal Balance Experiment. The 95% confidence limits are indicated.

FIG. 10 b. Oxygen consumption in cc/gm/hr of winter-caught shrews while exhibiting activity level 2 (interrupted sleep) in the Thermal Balance Experiment. The 95% confidence limits are indicated.

Statistic	O ₂ Consumption AL2	
	Winter	Summer
Regression Equation	$Y=4.7454-.0869(X-16.4305)$	$Y=5.3448-.1732(X-16.2310)$
No Obs	111	183
Std Error Estimate	1.2403	1.1345
Std Dev Slope	.0139	.0107
F-ratio Slope	39.24	263.46
Probability of significant difference in slopes	P<.01	

a.

b.

FIG. 11 a. Oxygen consumption in cc/gm/hr of summer-caught shrews while exhibiting activity level 3 (normal exploring activity) in the Thermal Balance Experiment. The 95% confidence limits are indicated.

FIG. 11 b. Oxygen consumption in cc/gm/hr of winter-caught shrews while exhibiting activity level 3 (normal exploring activity) in the Thermal Balance Experiment. The 95% confidence limits are indicated.

Statistic	O ₂ Consumption	
	Winter	Summer
Regression Equation	$Y=6.5425-.0516(X-12.0600)$	$Y=5.7949-.2364(X-16.9554)$
No Obs	168	125
Std Error Estimate	1.2900	1.2127
Std Dev Slope	.0113	.0123
F-ratio Slope	20.87	370.85
Probability of significant difference in slopes	P<.01	

a.

b.

FIG. 12 a. Metabolism of summer-caught shrews as a function of ambient temperature. Metabolism is calculated for a 20 gm, 70 cm² shrew with an RQ of .85; units are cal/animal/hr. These regression lines are based on oxygen consumption data as recorded in the Thermal Balance Experiment. Σ AL includes oxygen consumption data for all four locomotor activity levels. AL2 is restricted to oxygen consumption data recorded while the shrews exhibited activity level 2 (interrupted sleep). AL3 is restricted to oxygen consumption data recorded while the shrews exhibited activity level 3 (normal exploring activity).

FIG. 12 b. Metabolism of winter-caught shrews as a function of ambient temperature. Other conditions listed above are true for this case.

Statistic	Metabolism Σ AL	
	Winter	Summer
Regression Equation	$Y=583.83-7.53(X-13.68)$	$Y=544.86-20.37(X-16.33)$
No Obs	311	320
Std Error Estimate	154.62	132.49
Std Dev Slope	.9991	.8924
F-ratio Slope	56.91	520.17
Probability of significant difference in slopes	$P<.001$	

a.

b.

A winter-caught shrew at 3° C uses 525 cal/hr at activity level 2 and 705 cal/hr at activity level 3; an increase of 130 cal/hr. A summer-caught shrew at 23° C uses 400 cal/hr at activity level 2 and 465 cal/hr at activity level 3. Including oxygen consumption data for all activity levels, a summer-caught shrew at 3° C uses 145 cal/hr more than a winter-caught shrew at 3° C. The summer-caught shrew's metabolism increases 20.37 cal/hr/°C, whereas the winter-caught shrew's metabolism increases 7.53 cal/hr/°C.

Metabolism is a measure of heat production. The difference between the fur surface temperature and the ambient temperature is a measure of heat transfer (Fig. 13). At 3.0° C a winter-caught shrew has a fur surface temperature of 3.9° C, whereas the summer-caught shrew has a fur surface temperature of 4.1° C. The summer-caught shrew is losing more heat than the winter-caught shrew. The heat production of the summer-caught shrew must be higher in order for it to achieve a thermal steady-state.

The Thermal Balance experiment was based on the model of Porter and Gates (1969):

$$\text{Heat gain } (H_g) = \text{Heat loss } (H_l)$$

FIG. 13. Regressions of Δt (fur surface temperature - ambient temperature) on ambient temperature for summer-caught shrews (dashed line) and winter-caught shrews (solid line). The 95% confidence limits are indicated for each regression line.

Statistic	Δt	
	Winter	Summer
Regression Equation	$Y = .6103 - .0291(X - 13.6764)$	$Y = .6616 - .0346(X - 16.3293)$
No Obs	311	320
Std Error Estimate	.1306	.0974
Std Dev Slope	.0008	.0007
F-ratio Slope	193.92	793.50
Probability of significant difference in the slopes	$P < .001$

$$M + Q_{abs} = \epsilon \sigma T_r^4 + h_c(T_r - T_a) + E_{ex} + E_{sw} \pm C + W$$

All of the terms in the equation are expressed in cal/cm²/min; all temperatures are in absolute degrees.

The components of the terms are defined as follows:

M is the metabolism of the animal,

Q_{abs} is the amount of radiation absorbed by the animal surface,

ϵ is the emissivity of the fur surface,

σ is the Stefan-Boltzmann constant,

T_r is the surface temperature of the radiating outermost surface,

T_a is the air temperature,

h_c is the convection coefficient,

E_{ex} is the amount of energy lost by respiratory moisture loss,

E_{sw} is the amount of energy lost by sweating,

C is the heat conducted to the substrate,

W is the thermal equivalent of work done by the animal.

For animals smaller than 10 cm diameter possessing small appendages, their appendage surface area is neglected. The total surface area is divided into the metabolic rate in cal/min to obtain heat production per unit area. An animal receives in the natural habitat several streams of radiation including direct sunlight, S , skylight, s , reflected sunlight, $r(S + s)$ where r is a term for reflectivity, infrared thermal radiation emitted by the soil, rock, and vegetation surfaces of the environment, R_g ,

and from the atmosphere, R_a . These radiations, R_i , are of various intensities and spectral compositions. The animal surface presents various areas, A_i , to the different incident fluxes of radiation. The animal surface absorbs the various incident fluxes with mean absorptivities, $\bar{a}_i$. The amount of radiation absorbed, Q_{abs} , by animal is given by:

$$Q_{abs} = \bar{a}_1 A_1 S + \bar{a}_2 A_2 S + \bar{a}_3 A_3 r(S+s) + \bar{a}_4 A_4 R_g + \bar{a}_5 A_5 R_a .$$

In the Thermal Balance experiment:

(1) Q_{abs} : Both incoming and reradiated thermal energy were measured at each test temperature with the net radiometer. Due to the air flow design of the environmental cabinet and the subdued lighting used, the net radiation flux was zero ($R_a = R_g$). The shrew was exposed to the thermal radiation, R , equally over the entire body surface, A . The area of the animal surface was assumed to be constant at 70 cm^2 for all shrews tested. Porter and Gates (1969) measured a mean absorptivity of .8 for Sorex. It was assumed that the absorptivity of Sorex and Blarina is the same since the two species of shrews have fur of the same color and texture.

(2) M : Metabolism was estimated from oxygen consumption data. Metabolism was calculated in $\text{cal/cm}^2/\text{min}$, assuming a 20 gm, 70 cm^2 surface area shrew with an RQ of .85.

(3) ϵT_r^4 : The emissivity of the fur surface, ϵ , was measured for Sorex by Porter and Gates (1969).

The Stefan-Boltzman constant, σ , is 0.817×10^{-10} cal/cm²/min/deg⁴. The surface temperature, T_r , of the outermost surface was measured directly in the experiment.

(4) $h_c(T_r - T_a)$: The convection coefficient, h_c , is expressed as $h_c = k \frac{V^{.33}}{D^{.66}}$, where V is the wind speed in cm/sec, D is the diameter of the animal's body in cm, and k is a constant which has units such that h_c is in cal/cm²/min/deg. The constant k is a complex term which should be evaluated experimentally for the animal; however, Gates (1962) and Porter and Gates (1969) state that the body shape of most animals may be approximated by a cylinder. For a smooth cylinder with axis perpendicular to the direction of wind flow, $k = 6.17 \times 10^{-3}$ (Gates, 1962). In the experiment, the wind speed in the metabolism chamber was measured to be 20 cm/sec. The diameter of the shrew's body was assumed constant at 2 cm. The surface temperature of the outermost surface, T_r , and the air temperature, T_a , were measured directly.

(5) E_{ex} & E_{sw} : Chew (1951) measured insensible loss of water (E_{ex} & E_{sw}) for Blarina over a range of temperatures from 18° to 28° C. Chew found a water loss of about 0.01 cc/cm²/day/°C. From this data, water loss is calculated as $H_2O = 0.01 + 0.0015(T_a)$, where H_2O is water loss in cc/cm²/day and T_a is the air temperature. The latent heat of vaporization of water may be calculated according to the equation: $H_{vap} = 595.9 - 0.56(T_w)$, where H_{vap} is

the heat of vaporization in cal/gm and T_w is the temperature of the water in °C (Kleiber, 1961). The water loss, expressed in cc/cm²/min, multiplied by the heat of vaporization of water in cal/cc, gives the energy loss in cal/cm²/min.

(6) C & W: Under the conditions of the experiment, heat conducted to the substrate, C, and the external work done by the animal, W, were assumed to be negligible.

All energy quantities used in the model are in cal/cm²/min; however, these variables have been expressed in cal/animal/hr, for a 20 gm shrew with a surface area of 70 cm². Division of the graphical values by 4200 gives the original units. All temperatures used in the model are in absolute degrees, but all analyses are presented using centigrade degrees.

The results from the model are found in Figure 14 for summer-caught shrews and Figure 15 for winter-caught shrews.

(1) Q_{abs} : The incoming thermal radiation was the same for both summer and winter-caught shrews.

(2) M: Winter-caught shrews had a metabolism of 7.53 cal/hr/°C, whereas summer-caught shrews had a metabolism of 20.37 cal/hr/°C.

(3) $\epsilon \sigma T_r^4$: Heat loss by radiation was similar. Summer-caught shrews lost 25.51 cal/hr/°C, and winter-caught shrews lost 25.63 cal/hr/°C.

(4) $h_c(T_r - T_a)$: Heat loss by convection was 1.33 cal/hr/°C for summer-caught shrews and 1.11 cal/hr/°C for winter-caught shrews.

(5) E_{ex} & E_{sw} : Heat loss by evaporation was the same since the same estimate for water loss was used for both cases. Heat loss by evaporation was 2.52 cal/hr/°C.

(6) Total Heat Gain: The summer-caught shrews had a total heat gain expressed as H_g in cal/hr = $1870 + 10.10(T)$, where T is ambient air temperature from 0° to 25°C. The winter-caught shrews had a total heat gain expressed as $H_g = 1700 + 22.95(T)$.

(7) Total Heat Loss: The summer-caught shrews had a total heat loss expressed as H_l in cal/hr = $1610 + 26.70(T)$, where T is ambient air temperature from 0° to 25°C. The winter-caught shrews had a total heat loss expressed as $H_l = 1600 + 27.04(T)$.

(8) Thermal Equilibria: To achieve a thermal steady-state H_g must equal H_l . Net heat exchange is the difference in H_g and H_l . The 95% confidence limits shown for total heat gain (H_g) in Figures 14 and 15 are the limits around the estimates of metabolism (M). No limits were actually determined for total heat loss (H_l).

FIG. 14 a. Primary components of heat gain and heat loss for summer-trapped shrews as tested in the Thermal Balance Experiment. $\epsilon\sigma T_r^4$ is radiation loss, Q_{abs} is radiation absorbed, and M is the metabolism of the animal. The 95% confidence limits are indicated for the estimates of metabolism (M). All units are cal/animal/hr, for a 20 gm, 70 cm² shrew with an RQ of .85.

FIG. 14 b. Total heat gain (H_g) and total heat loss (H_l) for summer-trapped shrews as tested in the Thermal Balance Experiment. Net heat exchange = $H_g - H_l$.

$$H_g = M + Q_{abs}$$

$$H_l = \epsilon\sigma T_r^4 + hc(T_r - T_a) + E_{sw} + E_{ex}$$

Details of these expressions are discussed in the text. The 95% confidence limits for estimates of metabolism (M) are shown for the estimates of total heat gain (H_g). All units are cal/animal/hr, for a 20 gm, 70 cm² shrew with an RQ of .85.

FIG. 15 a. Primary components of heat gain and heat loss for winter-trapped shrews as tested in the Thermal Balance Experiment. $\epsilon\sigma T_r^4$ is radiation loss, Q_{abs} is radiation absorbed, and M is the metabolism of the animal. The 95% confidence limits are indicated for the estimates of metabolism (M). All units are cal/animal/hr, for a 20 gm, 70cm² shrew with an RQ of .85.

FIG. 15 b. Total heat gain (H_g) and total heat loss (H_l) for winter-trapped shrews as tested in the Thermal Balance Experiment. Net heat exchange = $H_g - H_l$.

$$H_g = M + Q_{abs}$$

$$H_l = \epsilon\sigma T_r^4 + hc(T_r - T_a) + E_{sw} + E_{ex}$$

Details of these expressions are discussed in the text. The 95% confidence limits for estimates of metabolism (M) are shown for the estimates of total heat gain (H_g). All units are cal/animal/hr, for a 20 gm, 70 cm² shrew with an RQ of .85.

Postural behavior of the shrews tested in the Thermal Balance experiments was observed as the ambient temperature decreased down a linear ramp from 28° to 0° C. Although records of these behavioral changes were qualitative, three fairly distinct postures were observed. These results are in Table 8. On the warm end of the ramp, summer-caught shrews stop using behavioral thermoregulation for cooling at about 27° C. The winter-caught shrews do not stop using such tactics until about 24° C. At about 15° C the summer-caught shrews start using behavioral thermoregulation to conserve heat. The winter-caught shrews do not use heat-conserving behavior until a temperature of about 6° C is reached. At the 6° C behavioral change point of the winter-caught shrews, the mean metabolism was only slightly higher (63 cal/hr) than at the 24° C behavioral change point. Within this 18 degree temperature range, thermoregulation may be primarily behavioral, not metabolic. At the 15° C behavioral change point of the summer-caught shrews, mean metabolism was 218 cal/hr higher than at the 27° C behavioral change point. Within this 12 degree temperature range, thermoregulation is both behavioral and metabolic.

TABLE 8
POSTURAL BEHAVIOR OF SHREWS
IN THE THERMAL BALANCE EXPERIMENT

Statistic	Season of Capture			
	Summer	Winter	Summer	Winter
	Postural Behavior Change			
	S → N	S → N	N → C	N → C
No. Obs	8	8	8	8
$\bar{x}$ T	27.3	23.8	15.3	6.1
SD	1.1	1.4	1.8	2.7
$\bar{x}$ Δ T	0.34	0.30	0.66	0.78
SD	0.05	0.05	0.10	0.04
$\bar{x}$ M	332	599	550	662
SD	60	201	103	78

$\bar{x}$ T is mean ambient temperature in °C.

$\bar{x}$ Δ T is mean Δ T (fur surface temperature - ambient temperature) at $\bar{x}$ T.

$\bar{x}$ M is mean metabolism for a 20 gm, 70 cm² surface area shrew with an RQ of .85 at $\bar{x}$ T.

S is a spread posture.

N is a normal, sitting posture.

C is a spherical posture.

Carcass Cooling

In all cases tested cooling was very rapid at first when the temperature gradient was high and became slower as the body temperature approached the ambient temperature. The rate of cooling of an object under such conditions is proportional to a cooling constant and to the temperature differential between the body and its surroundings. Thus $\frac{dT_b}{dt} = \beta(T_b - T_a)$, where T_b is body temperature, t is time, β is the cooling constant, and T_a is the ambient temperature. If this expression is valid in the present situation, a plot of $\log(T_b - T_a)$ as a function of time should yield a linear relation of the form: $\log |T_b - T_a| = c + \beta t$, where c is the integration constant. The F-ratio of the slope of the regression line shows a very high degree of linearity in all three cases (Fig. 16). The fall in temperature of the body is related to the loss of heat by the expression: $\Delta T_b = \frac{\Delta q}{(Sp)(w)}$, where T_b is body temperature in degrees, q is heat in calories, Sp is the specific heat of the body in cal/gm/°C, and w is the weight of the body in grams. Thus $\frac{dq}{dt} = C_{ht}(T_b - T_a)$, where $C_{ht} = (Sp)(w)(\beta)$. The coefficient of heat transfer, C_{ht} , in cal/gm/hr/°C is referred to as the thermal conductance of the body by some authors.

FIG. 16. Seasonal differences in the cooling rates of shrew carcasses. The regression lines of $\log(T_b - T_a)$ on elapsed time are illustrated for shrews trapped in summer (long dashed line), fall (short dashed line), and winter (solid line). T_b is the body core temperature. T_a is the ambient temperature.

Statistic	Summer Shrews	Fall Shrews	Winter Shrews
No carcasses	10	10	10
Regression Equation	$Y = .9750 - .0183(X - 33)$	$Y = 1.0022 - .0172(X - 33)$	$Y = 1.0819 - .0143(X - 33)$
Std Error Estimate	.0089	.0060	.0047
Std Dev Slope	.0005	.0003	.0003
F-ratio Slope	1268.92	2423.54	2757.98
Probabilities of significant differences in slope:			
	Summer-Fall P<.10	Summer-Winter P<.01	Winter-Fall P<.01
Calculated Values	Summer Shrews	Fall Shrews	Winter Shrews
Cooling Constant (°C/hr)	-2.5269	-2.3729	-1.9797
Heat Transfer (cal/gm/hr/°C)	-2.0937	-1.9696	-1.6432

The cooling constants measured in the Carcass Cooling experiment were converted to heat transfer coefficients in units of $\text{cal/gm/hr/}^{\circ}\text{C}$ by using the specific heat of whole white mice, $0.83 \text{ cal/gm/}^{\circ}\text{C}$ (Hart, 1951), and the individual's body weight. These measures of heat transfer include the thermal properties of the body tissues, fat layers, and the fur layer. The summer-caught shrews had the highest heat loss; the winter-caught shrews, the lowest (Fig. 16). For a 20 gm animal heat loss from (1) a summer-caught shrew would be $41.95 \text{ cal/}^{\circ}\text{C/hr}$, (2) a fall-caught shrew, $39.39 \text{ cal/}^{\circ}\text{C/hr}$, and (3) a winter-caught shrew, $32.86 \text{ cal/}^{\circ}\text{C/hr}$. The summer-caught shrews have a 21.66% increase in heat loss above that of the winter-caught shrews.

Systems Analysis

A deterministic model of the energy dynamics of this predator-prey system is proposed. This model is built as a series of sections (subsystems). Each subsystem is described mathematically and all are organized in a way that allows a routine procedure for solution. The model is primarily descriptive and secondarily, predictive. It was designed to be realistic and precise, but not general. Much of the data are suitable for the development of a stochastic model, which will be attempted at a later date.

The model of the thermal balance of an individual predator is: $M + Q = R + C + E$ (Energy units: cal/cm²/hr)

$$\begin{aligned} M &= M_t + M_a & Q &= f(t) \\ R &= f(t) & C &= f(t) \\ E &= f(t) & M_t &= f(t) \\ M_a &= f(A) & A &= f(h) \end{aligned}$$

$$t = f(h)$$

where:

t = soil:leaf litter interface temperature in °C

h = time in hours

E = thermal energy loss by evaporation

C = thermal energy loss by convection

R = thermal energy loss by radiation

Q = thermal energy gain by absorption

M = thermal energy production by total metabolism

M_t = metabolic rate due to thermoregulation

M_a = metabolic rate due to locomotor activity

A = amount of daily locomotor activity.

These are complex functions of several factors besides temperature. The assumptions required to satisfy these relations are discussed in the section on the Thermal Balance experiment.

The relation $t = f(h)$ for summer temperatures at the soil:leaf litter interface is presented graphically in Figure 17. Under winter conditions, $t = 0^\circ \text{C}$. The relation $A = f(h)$ for both seasons is presented in Figure 18.

FIG. 17. Summer temperatures at the soil-leaf litter interface as a function of time.

$$T = 18.0 + 3.0 \cos D$$

$$D = \pi b + (\pi c t) / 12.0$$

T is temperature in °C

t is time in hours

b & c are arbitrary constants

$$b = 1.15; c = 0.70$$

Calculated values of T (°C) are illustrated by ▲.

The vertical bars indicate the 95% confidence limits about the mean temperatures at the soil-leaf litter interface as measured in the Manotick woodlot during 12-20 August.

The open circles indicate the range of temperatures measured at each time interval at the soil-leaf litter interface in the Manotick woodlot during 12-20 August.

FIG. 18. Model of locomotor activity distribution.

$$AL = 1. + (.2X + c X^2)(|\sin X|)$$

$$X = |(\pi/12)(t) - \pi|$$

t is time in hours

c is an arbitrary constant; higher values increase the intensity of activity while retaining a similar distribution pattern in time.

The model starts at 0100 hours and continues to 2400 hours. The two sides of the expression should balance approximately for each hour. Total metabolism, M , represents the part of the metabolizable energy that the individual uses for maintenance per day under these conditions.

The individual predator's daily chemical energy budget is represented by:

$$I = P + F + M \quad (\text{Energy units: kcal/animal/day})$$

where:

I = energy of ingested food

P = energy used in growth and reproduction

F = energy lost in feces and urine

M = metabolic energy.

Energy transfer from prey to predator is represented by:

$$ER = I + LR \quad (\text{Energy units: kcal/animal/day})$$

where:

ER = energy of prey required by a predator

I = energy of ingested food

LR = energy lost in prey residues.

Expanding to the population level for a season results in:

$$\begin{aligned} PEU &= (S)(D)(ER) & (\text{Energy units: kcal/} \\ PER &= PEB - PEU & \text{predator population/} \\ & & \text{season}) \end{aligned}$$

where:

PEU = total prey energy used by the
predator population

S = number of individuals in the
predator population

D = number of days

ER = daily prey energy requirement of an
individual predator

PER = prey population energy remaining unused

PEB = prey population energy base.

A number of assumptions have been made:

- (1) Within a given season, the temperature and thermal characteristics of the environment are the same from one day to the next.
- (2) Individual productivity is constant at 145 cal/day, as estimated in the discussion of Blarina productivity.
- (3) Loss of prey energy in residues is constant at 10%.
- (4) The energy flow through the predator population is equal to the sum of the energy flows through all the individuals.
- (5) Within a season the predator population energy flow is the same for each day.
- (6) Within a season the predator population remains at a constant size.

- (7) Within a season the prey population energy content does not increase.
- (8) Blarina is the sole consumer of the prey.
- (9) A year consists of two seasons, referred to as summer and winter, and each is 182 days in length.

DISCUSSION

Thermal Environment

Pruitt (1953) states that the forest floor from one to six inches deep is the zone of the habitat most used by Blarina. Live trap captures indicate that Blarina usually do not travel on the leaf litter surface during the day in the summer or on the snow surface in the winter. The temperature limits that a Blarina would experience annually are approximately equal to the annual temperature limits of the leaf litter layer. Pruitt (1953) measured humus temperatures at a depth of three inches in a hardwood forest in the northern part of the lower peninsula of Michigan. The annual temperature limits were 0° to 20° C. Pruitt (1959) measured leaf litter temperatures in several areas of the George Reserve, Michigan. Pruitt's earlier study area in northern Michigan has permanent winter snow cover, whereas the George Reserve has only intermittent snow cover. In the dry hardwoods of the George Reserve, the absolute minimum temperature at three inches below the surface was -1° C, and the absolute maximum temperature at that depth was 22° C. Jameson (1949) found that

temperatures in small mammal tunnels in central New York during the winter deviated little from 0° C. Getz (1961) found that temperature becomes a factor in the local distribution of Blarina only in those areas in which vegetation is sparse.

In the Manotick woodlot the annual air temperature may be from -30° to +30° C. The forest canopy and the leaf litter in the summer and the snow and leaf litter in the winter are effective in moderating temperatures at the soil-leaf litter interface; there the annual range is 0° to 24° C (Fig. 2).

Gates (1962) states that the downward stream of atmospheric radiation from a clear daytime sky at an air temperature of 30° C is 0.56 cal/cm²/min. On a clear night, with an air temperature of 15° C and average humidity conditions, the downward stream of infrared thermal radiation from the atmosphere is 0.44 cal/cm²/min. If the night sky is overcast and the air temperature is 15° C, the downward flux is 0.53 cal/cm²/min. These values are for incoming radiation on a horizontal surface in the latitude zone 40° to 50°. Moen (1968a) measured a downward radiation flux of 0.425 cal/cm²/min under clear skies at 0° C at night in a hardwood forest in Minnesota. Moen (1968b) measured a downward radiation flux of 0.481 cal/cm²/min under a birch tree in Minnesota between 2100 and 2400 hours in August. The upward

radiation (terrestrial) flux was $0.510 \text{ cal/cm}^2/\text{min}$ in the same location at the same time.

During August in the Manotick woodlot, the mean maximum incoming radiation was $0.546 \text{ cal/cm}^2/\text{min}$ (Fig. 4). Incoming radiation on clear, sunny days at 1200 to 1300 hours reached $0.800 \text{ cal/cm}^2/\text{min}$. This level occurred only on those occasions and was never exceeded. The mean minimum incoming radiation was $0.375 \text{ cal/cm}^2/\text{min}$. The mean maximum terrestrial radiation was $0.536 \text{ cal/cm}^2/\text{min}$. The mean minimum terrestrial radiation was $0.406 \text{ cal/cm}^2/\text{min}$.

Geiger (1965) states that according to the Stefan-Boltzman law the radiation emitted by the soil surface by day and by night would vary as T^4 , since the ground acts as a black body. Snow and ice also behave toward long-wavelength radiation practically as black bodies (Geiger, 1965). Therefore the radiation environment at the soil surface under the snow cover may be calculated approximately from the temperature at the soil surface. In February the soil temperature was 0° C under the snow cover; the radiation flux would be $0.294 \text{ cal/cm}^2/\text{min}$.

Unless the shrew was exposed to direct, bright, summer sunshine or to very cold, clear, night skies, the annual radiation flux limits in its environment would be 0.294 to $0.546 \text{ cal/cm}^2/\text{min}$.

The Prey and Predation

Except for a few spiders, all prey organisms were caught in the pit traps during the night. The mean nightly capture of the 12 flower pot pit traps was 6.23 kcal (SD = 4.15) during August (Table 1). The mean nightly capture of the 10 funnel pit traps was 1.51 kcal (SD = 1.49) during August (Table 2). Both types of traps were operated simultaneously and in comparable areas. The two types of traps caught the same types of prey. The mean nightly capture of the funnel pit traps is 24% of the mean nightly capture of the flower pot pit traps. The sum of the perimeters of the funnel pit traps (251.2 cm) is only 33% of the sum of the perimeters of the flower pot pit traps (753.6 cm). This difference in the total perimeter appears largely responsible for the differences in the captures. Estimates of prey density from pit trap captures is highly dependent on prey activity and pit trap selectivity. The mean nightly captures in September were 1.72 kcal and 0.467 kcal, for the flower pots and funnels, respectively (Tables 1 & 2). These September captures seem to indicate a decrease in prey density from the August levels. This decrease in mean nightly captures appears to be the effect of cooler temperatures on arthropod activity, not an actual reduction in prey density. On two warm nights during September, the nightly captures were as high as on an August

night. The wide variances about all of the mean nightly captures are due to slightly different compositions of prey as well as the differences in the total number of prey caught each night.

The 10 funnel pit traps were evenly distributed in the 4 m² area of the Open Control enclosure. As this "enclosure" delineated an area of the forest floor and did not restrict prey mobility, the funnel pit trap captures are an indication of the prey activity in that area each night. The actual relation of number of prey per 4 m² of forest floor at a specific time to the number of prey captured per 10 funnel pit traps per night is unknown. The total area of the 10 funnel pit traps is 1.26% of the area of the enclosure. The small size of the funnel pit traps allowed their installation with minimal disturbance of the forest floor. However because of the small size of these pit traps, their captures may underestimate the numbers of prey actually moving in the 4 m² area. The nightly captures of the funnel pit traps indicate the minimum number of prey in the 4 m² area. In August a mean minimum estimate of 0.378 kcal of prey was present in one square meter of forest floor each night (Table 2).

The winter prey sample contained 33.473 kcal/4 m² (Table 3). Comparison of total prey availability in summer and winter is made difficult by the differences

in sampling techniques as well as differences in life history stages of the prey. The winter sample included several species which were never caught in the pit traps. Some species were found as larvae in the winter and as adults in the summer.

Changes in prey activity further complicate the seasonal comparison. Except for a few spiders, no prey were caught in the flower pot pit traps during the entire winter trapping period. Since there is essentially no movement of the prey in the winter and the winter sample was a total count of the potential prey in 4 m^2 , those prey are the total energy supply of that area for the entire winter. No immigration or reproduction of prey occurs to replenish the energy content removed by a predator. In contrast, the prey energy supply of an equivalent area in the summer is characterized by the immigration and emigration of the prey. This movement of prey typically occurs from mid-April until mid-October. Using flower pot pit traps in several locations near Ottawa, some of which are comparable to the Manotick woodlot, Barlow (1970) trapped Pterostichus species throughout this six month interval. In a current project, flower pot pit captures are collected weekly from the Manotick woodlot. Although the species composition of the captured prey changes somewhat from week to week, the total numbers of prey captured each week are fairly

consistent. The 4 m² area of the Open Control enclosure had a mean nightly capture of 1,510 kcal (Table 2). That amount of prey energy could be removed from 4 m² each night for the six summer months; which would amount to 67,950 kcal removed from each square meter. Daily mean energy catches of several species are expanded to a 182-day summer season in Table 9. This table compares the total prey energy available from one square meter of forest floor for each season.

Extrapolation from the prey energy content of one square meter of forest floor to the total prey energy content of the entire woodlot may be done, assuming that (1) the samples are representative, and (2) the woodlot is homogeneous. While no quantitative estimates exist to support these assumptions, a qualitative evaluation indicated that both are fairly well met. The energy content of the prey in the entire Manotick woodlot for the 182-day winter season is estimated at 219×10^6 cal. If every square meter of the woodlot could yield 67,950 kcal/season, as did the square meter discussed earlier (Table 9), the energy content of the prey in the entire woodlot for the 182-day summer season would be 1779×10^6 calories.

The food habits of Blarina have been investigated by a number of authors. Hamilton (1930) examined the gut contents of 244 Blarina. Captures were made every

TABLE 9
SEASONAL COMPARISON OF AVAILABLE PREY ENERGY

Organism	kcal/m ² in	
	Winter	Summer
<u>Carabus</u>		14.310
<u>Pterostichus</u>		3.420
<u>Calathus</u>		3.015
<u>Ceuthophilus</u>		30.870
<u>Acrosternum</u>	1.736	
<u>Vespula</u>	0.223	
<u>Mesodon</u>	0.660	
Julida	0.850	1.485
Lycosidae	0.294	4.320
Henricopidae	0.247	
Elateridae larvae	1.214	
Tipulidae larvae	0.673	
Lepidoptera larvae	0.070	
Carabidae larvae	0.135	
Noctuidae pupae	0.329	
Annelida	1.936	2.745
Other Araneae		7.785
Σ	8.387	67.950

month of the year in a variety of locations near Ithaca, New York. Insects were found in 47.8% of the stomachs, plant material in 11.4%, and the remainder was mostly small percentages of annelids, molluscs, crustaceans, and centipedes. Vertebrate remains were in only 4.1%. Hamilton also examined the gut contents of 66 Blarina taken from 15 December to 15 March. Insects were found in 58.6% of the stomachs, plant material in 25.3%, vertebrates in 7.6%, and annelids, etc., the remainder. Whitaker and Ferraro (1963) examined 221 Blarina stomachs taken in the summer near Ithaca, New York. More earthworms, slugs and snails were found than in studies by Hamilton. No small mammals were found. Eadie (1944) did fecal analyses of Blarina in the winter near Ithaca. He found that very little plant material was eaten and that mice, primarily Microtus pennsylvanicus, constituted a large proportion of their diet. All authors agree that Blarina will eat practically any small animal which it encounters. Food preference studies in the laboratory indicate that the Blarina in the present study act no differently. Both Peromyscus and Clethrionomys were offered as potential prey to Blarina, but there was never any evidence in the laboratory or the field that Blarina was preying upon either of these mice.

Shull (1907), Hamilton (1930), Buckner(1964), and Martinsen (1969) have commented on Blarina's tendency

to hoard and store various types of foods. This storage behavior was characteristic of the Blarina in the present study. In the Functional Response experiments, where the prey (Tenebrio larvae) were recovered daily, typically all remaining larvae were found in a clump in or near the Blarina's leaf nest. In one Food Preference test, after about two hours in the test enclosure, a Blarina bit through the thorax of three Carabus and then stacked the immobilized bodies in a corner of the box. Later they were eaten.

The daily food consumption of Blarina has been estimated by a number of investigators. Early papers (Shull, 1907; Babcock, 1914; Hamilton, 1930) report consumption only in terms of grams eaten. Table 10 presents details of more recent investigations where the energy contents of the food are reported in kcal eaten per animal per day. Food consumption in the various experiments of the present study are summarized in Table 11.

Sealander (1952) found that Peromyscus previously kept at warm temperatures had higher rates of food consumption after about 15 days at intermediate and low temperatures than did mice previously kept at cool temperatures. Sealander concluded that the "warm" mice compensated for their reduced insulative efficiency at low temperatures by increasing their rate of heat

TABLE 10
DAILY FOOD CONSUMPTION OF BLARINA
AS DETERMINED BY OTHER INVESTIGATORS

Temp (°C)	Food Type	Amount (kcal)	Reference
25°	beef liver	13.7-15.9	Morrison <u>et al.</u> , 1957
5°	beef liver	17.8-19.7	"
9°-14°	dog food	10.8	Buckner, 1964
9°-14°	larch sawfly	12.0	"
22°-24°	mealworms	6.0	Martinsen, 1969

TABLE 11
SUMMARY OF FOOD CONSUMPTION EXPERIMENTS

Expt. Name	Source	Capture Season	Test Temp. (°C)	Test Duration	Approx. kcal Avail.	kcal Eaten $\bar{X}$ (SD)
Nat. Food Preference	p. 41	Summer	23°	12 hrs	5	4.49 (.08)
Nat. Food Consumption	p. 42	Summer	23°	12 hrs	5	4.21 (.30)
Field Enclosures	Table 4	Summer	Summer	24 hrs	4	2.81 (.09)
Functional Response (Constant)	p. 48	Winter	Summer Winter	24 hrs	22	8.37 (4.15) 9.35 (4.95)
Functional Response (Variable)	Fig. 7	Winter	Summer Winter	24 hrs	15	10.20 (1.80) 13.80 (1.20)
Assimilation	Table 5	Summer	3° 20°	8 hrs	20	6.74 (3.25) 7.64 (2.31)
		Winter	3° 20°			10.05 (3.98) 6.53 (3.07)

production through increased food consumption. Wolk (1969) found that the absolute food intake of Sorex araneus during the winter was only 9.7% higher than in the summer. Morrison, Pierce, and Ryser (1957) found a slight increase in daily food consumption of Blarina when kept at 5° C. However, details of season of capture and acclimation period prior to testing are not given. In the Functional Response experiment, when variable food supplies were provided each day, winter-caught shrews had a slightly higher food consumption under winter conditions than under summer conditons (Figs. 6 & 7). There were no significant differences in food consumption among the four test conditions in the Assimilation experiment (Tables 5 & 6).

Holling (1959) examined the functional response of Blarina to cocoons of the European pine sawfly, Neodiprion sertifer. For an increase from 10^5 cocoons per acre to 2×10^5 cocoons per acre, Blarina opened an additional 130 cocoons. Above 3×10^5 cocoons per acre no functional response of Blarina was seen. Buckner (1964) noted the functional response of Blarina to numbers of eonymphs of the larch sawfly, Pristiphora erichsonii. When 200 eonymphs were offered, the Blarina ate 194 of them. When 400 eonymphs were offered, the Blarina would take only about 300 eonymphs; however, wastage and hoarding of additional eonymphs then occurred.

Using variable food levels in the Functional Response experiment, the same pattern of functional response was found. When the number of Tenebrio larvae was raised, the Blarina ate additional larvae (Figs. 6 & 7). The highest number of larvae offered was 100, but never more than 86 were eaten. The intercepts of the response curves under winter conditions are only slightly higher than the intercepts of the response curve under summer conditions and the slopes of these lines are not significantly different (Figs. 6 & 7).

Morrison, Pierce, and Ryser (1957) and Buckner (1964) concluded that Blarina consumes only what is required for metabolism. In the present study, when Blarina were kept for several months in the laboratory at 23° C, they typically gained 3 to 5 grams body weight. Dissection of such individuals upon death revealed large amounts of subcutaneous fat. Shrews kept for several months at 3° C typically did not change body weight. No large differences in body weight were found in fresh, trap-killed shrews caught during the summer, fall, or winter. Food consumption above the metabolic requirement and thus deposition of large amounts of fat seems to occur only after extended periods of "easy living" in the laboratory.

Assimilation

Digestible energy is the energy content of the food less the energy content of the feces. Digestive efficiencies are typically high for small mammals. Barrett (1969) reported a mean value of .90 for a least shrew (Cryptotis parva) eating newborn laboratory mice. Brisbin (1966) found the mean digestive efficiency of a hoary bat (Lasiurus cinereus) to be .91 when eating Tenebrio. The digestive efficiency of the least weasel (Mustela rixosa) when eating Microtus pennsylvanicus was .90 (Golley, 1960).

The diet appears to be the most important factor in determining digestive efficiency. Buckner (1964) found that Blarina had a digestive efficiency of .78 when eating larch sawfly eonymphs and .92 when eating canned dog food. Sharp (1967) fed a variety of diets to rice rats (Oryzomys palustris); the lowest digestive efficiency (.88) was when eating Spartina grass and the highest (.95) was when eating either Tenebrio larvae or sunflower seeds. The digestive efficiencies of the field mouse (Apodemus flavicollis) ranged from .93 when eating hazelnuts to .81 when eating acorns (Drozdz, 1967).

Metabolizable energy is the gross energy content of the food less the energy lost in feces and urine. The subtraction of the energy content of the urine is

necessary because the nitrogenous end-product of protein metabolism is primarily urea, not the oxides of nitrogen characteristic of the bomb calorimeter. Metabolic processes do not break down proteins to their lowest energy state; the bomb calorimeter does. A variable fraction of metabolizable energy appears as heat soon after ingestion; this is referred to as the specific dynamic action (SDA) or the calorogenic effect. It is believed to result from the exothermic reactions of intermediary metabolism in the interconversion, transportation, and storage of food molecules (King and Farner, 1961). The difference in metabolizable energy and the SDA is the energy available to the animal for maintenance, growth, and reproduction. Below thermoneutrality the heat production of the SDA may be used in maintaining the body temperature, and thus is not subtracted from the estimate of metabolizable energy. Metabolizable energy is the most precise estimate of the energy available to the animal for maintenance, growth, and reproduction. The ratio of metabolizable energy to gross food energy is referred to as assimilation efficiency. Often in the computation of this ratio the correction for the energy content of the urine is not made because the collection of urine is difficult. Unfortunately, some investigators determine the digestive efficiency of an animal and report the value as the assimilation efficiency. Drozd (1967) emphasizes the

distinction and reports both efficiencies for two small rodents eating different plant materials. On the average, the assimilation efficiency was 3% lower than the digestive efficiency. In the Assimilation experiment, the summer-caught shrews had an average assimilation efficiency of .76 and the winter-caught shrews had an average assimilation efficiency of .83. The assimilation efficiency is 10% lower than the digestive efficiency for the summer-caught shrews and 7% lower for the winter-caught shrews.

In the Natural Foods Consumption experiment, digestive efficiency was .83 (SD = .05) for four Blarina eating Carabid beetles. In the Assimilation experiment, standardized "shrewburgers" were used as food. There was no significant difference in digestive efficiency according to test temperature, but there was a significant difference according to the season of capture of the shrews (Table 6). Winter-caught shrews had an average digestive efficiency of .90, whereas summer-caught shrews had an average digestive efficiency of .85. There were no significant differences in metabolizable energy (Table 5).

Blarina is reasonably efficient in extracting metabolizable energy from its food. However, this process appears to function relatively independently of environmental influences.

Locomotor Activity

The lowest mean oxygen consumption measured was 3.58 cc/gm/hr. This was for summer-caught shrews at 23° C during deep sleep (Table 7). Martinsen (1969) found a mean oxygen consumption of 2.18 cc/gm/hr for Blarina under similar conditions. His measure of oxygen consumption during hyper-activity was 11.63 cc/gm/hr. Summer-caught shrews at 23° C when in hyperactive behavior consumed a mean of 7.41 cc/gm/hr (Table 7). The differences may be due primarily to the respirometry systems used. Martinsen used a short time-lag, closed-circuit system, which measured oxygen consumption on a per minute basis. The two minute time-lag in my open-circuit system tends to smooth variation. Pearson (1947) made seven 24 hr determinations of Blarina metabolism using a closed-circuit respirometer of similar design but with a slower response time than the system used by Martinsen. Pearson found minima of 3.6 to 4.6 cc/gm/hr, averages of 4.4 to 6.2, and maxima of 7.0 to 11.0.

Converting oxygen consumption into metabolic energy equivalents for a 20 gm shrew with an RQ of .85, the Locomotor Activity Costs experiments showed an increase of 126 cal/hr/activity level for summer-caught shrews. The slope of the regression line was 117 cal/hr/activity level for fall-caught shrews and 102 cal/hr/activity level for winter-caught shrews (Fig. 8).

Normal, exploring locomotion costs a shrew from 1.4 to 1.8 times as much as deep sleep. In general, mammals have a metabolic rate of moderate activity which is about double the minimum metabolic rate (King and Farner, 1961). Normal, exploring metabolism of Blarina is approximately 30 kcal/kg/hr. The cost of transport may be expressed as kcal/kg/km and is inversely proportional to velocity. If during normal, locomotor activity, a Blarina ran at a speed of 0.5 km/hr, then the total cost of transport would be 60 kcal/kg/km. On a per kilogram basis, Blarina's energy cost of transport is approximately equal to a Volkswagen automobile traveling at 1 km/hr (Tucker, 1970).

Most locomotor activity occurs between 1800 and 0600 hours during the night; very little occurs between 0600 and 1800 hours during the day. The nocturnal pattern is somewhat bimodal, with broad peaks about 2000 and 0400 hours (Fig. 9). This pattern agrees with Pearson's (1947) observation of two metabolic peaks, one early in the evening and one near dawn. Martinsen (1969) found a pattern of short bursts of activity between 1800 hours and about 1200 hours the next day. He found that Blarina were active only about 16% of 24 hours. Mann and Stinson (1957) estimated that Blarina were active only about 10% of 24 hours. Dixon (1970) examined the foraging and overall activity patterns of

Blarina both in the laboratory at constant temperatures and in the field under natural temperature conditions. He concluded that the shrews were predominantly nocturnal, although some activity occurs during the day. Dixon found a trend toward diurnal activity in winter-caught shrews tested outdoors under snow cover; these animals also showed a reduction in activity and an increase in duration of resting intervals. Only about two inches of snow covered the leaf litter layer in his test enclosure. The temperature range measured in the leaf litter was from -12° to $+8^{\circ}$ C. Although solar radiation was not measured, Dixon concluded that periods of high solar radiation on bright, clear winter days could account for the shift to diurnality.

Pearson (1947) and Platt (1969) note that Blarina are caught more frequently during the daytime in winter and at night in summer. In the Manotick woodlot the highest trap captures were on cool, damp nights during the summer and clear, mild days in the winter. Lower surface temperatures, increased moisture, and increased prey activity would favor a nocturnal pattern during the summer. During the winter Blarina could take advantage of solar heating, but this may occur only when the snow cover is thin or has been disturbed. Successful traps were those placed down through the snow to the leaf litter layer. Temperatures in the traps would be

warmer in the day than at night since they would be exposed to the ambient air temperatures and some sunlight would enter the snow cavity containing the trap. Higher trap temperatures could be responsible for the higher trap captures on clear, mild winter days. Traps set on the undisturbed surface of the snow were singularly unsuccessful; likewise no Blarina tracks or feces were ever observed on the snow surface. If the snow is deep and undisturbed, Blarina may remain under the snow and thus not be affected by solar radiation. Winter temperature records indicate that solar radiation has no daily influence on the leaf litter temperatures beneath approximately 80 cm of snow. Under these circumstances Blarina might not exhibit a diurnal activity pattern.

Thermoregulation

There is no evidence that Blarina hibernates, becomes dormant, or undergoes a daily torpor. Doremus (1965) made rectal measurements of body temperature during four different periods of the day. He found the mean body temperature of 25 Blarina to be 38.5° C. A constant body temperature of 38° C has been assumed in the present study.

Even though homeothermy is usually defined as the maintenance of a constant body temperature over a wide range of environmental temperatures, the body temperature does not stay strictly constant, but rather, fluctuates

slightly within a narrow range. The maintenance of a steady-state heat content of the body depends upon complex feedfack systems which control production, transfer, and dissipation of heat (Hammel, 1968). The principal source of heat is metabolic processes (King and Farner, 1961). However, as seen in Figures 14 and 15, the thermal energy from the environment may be of considerable importance. Within the body, heat moves primarily by conduction and convection. From the surfaces of the body, heat is dissipated to the environment by radiation, convection, conduction, and evaporation. The thermoregulatory mechanisms which control this heat loss are (1) adjustments which typically require small expenditure of energy, such as changes in piloerection, vascularization, evaporation, and behavior, and (2) metabolic adjustments.

The seasonal thermoregulatory modifications induced by climate were examined in the Assimilation experiment (Tables 5 & 6) and the Thermal Balance experiment (Figs. 10-15). Metabolic data from the Assimilation experiment are presented with comparable data from the Thermal Balance experiment in Table 12. Acclimatization to winter conditions allows a metabolic decrease in the winter-caught shrews when exposed to cold temperatures. There is a 75 cal/hr decrease in mean metabolism of winter-caught shrews in the Assimilation experiment.

TABLE 12
SEASONAL DIFFERENCES IN METABOLIC THERMOREGULATION

Experiment	Test Temp. (°C)	Metabolism ($\bar{X} \pm 95\% \text{ c.l. in cal/hr}$)		
		Season of Capture		$\bar{X}$ S-W
		Summer	Winter	
Assimilation	3°	957 $\pm$ 58	882 $\pm$ 97	75
Assimilation	20°	540 $\pm$ 64	468 $\pm$ 54	72
Thermal Balance	3°	816 $\pm$ 27	664 $\pm$ 27	152
Thermal Balance	20°	470 $\pm$ 16	536 $\pm$ 21	-66

The 152 cal/hr decrease in mean metabolism of winter-caught shrews at 3° C in the Thermal Balance experiment represents a 19% "savings". The increase of 66 cal/hr in metabolism in winter-caught shrews at 20° C in the Thermal Balance experiment is due to a disproportionately higher level of locomotor activity in the winter-caught shrews at warm temperatures (Fig. 11).

Hart (1963) states that seasonal changes in many homeotherms have been shown to be associated with an increased energy expenditure and an increased capacity to maintain high rates of heat production during the winter. Winter-caught shrews at cold temperatures have a higher metabolism than summer-caught shrews at warm temperatures (Tables 5, 7, 12). The energy cost of thermoregulation at winter temperatures is estimated as (1) 342 cal/hr in the Assimilation experiment, (2) 234 cal/hr in the Locomotor Activity Costs experiment, and (3) 194 cal/hr in the Thermal Balance experiment. Hart (1957) suggests that for a physiological description of acclimatization, the idea that acclimatization enhances survival is useful. A criterion of survival in acclimatization to a cold climate is an extension of the lower environmental survival temperature. Although studies of Blarina's temperature limits were not conducted, acclimatization appears to contribute to survival. With the same food supply and at the same cold temperature,

a winter shrew could have a greater survival time than a summer shrew.

In a study of seasonally induced changes in Peromyscus, Hart and Heroux (1953) examined cold resistance, metabolism, and pelage insulation. Winter mice were much more resistant to low temperatures than summer mice. At 2° C oxygen consumption was significantly lower in winter mice as compared to summer mice. Pelage insulation was significantly greater in winter than in summer mice.

The measures of heat loss in summer and winter-caught Blarina as determined in the Carcass Cooling experiment are not just for the pelage, but also include the thermal properties of the body tissues and fat. The summer-caught shrews had a significantly higher heat loss than winter-caught shrews (Fig. 16). Assuming that the rate of heat production equals the rate of heat loss, i.e., a constant body temperature, heat loss in $\text{cal/cm}^2/\text{hr}/^\circ\text{C}$ may be determined by measuring metabolic heat production from oxygen consumption data. Estimates of heat loss from the Carcass Cooling experiment and estimates based on oxygen consumption data in the Thermal Balance experiment are summarized in Table 13.

TABLE 13
RATE OF HEAT LOSS*

Experiment	Summer Shrews	Winter Shrews	S - W	% $(\frac{S-W}{S})$
Carcass Cooling	0.5992	0.4695	0.1297	21.64
Thermal Balance (AL 2)	0.2405	0.1207	0.1198	49.81
Thermal Balance (AL 3)	0.3282	0.0717	0.2565	78.15
Thermal Balance (all AL)	0.2910	0.1075	0.1835	63.05

* Units are cal/cm²/hr/°C.

The absolute values of heat loss measured by carcass cooling and measured by oxygen consumption differ due to (1) variation in locomotor activity during the metabolism determinations, and (2) a constant body position of the carcasses as compared to the changing body positions of the live animals. Morrison and Tietz (1957) measured heat loss by carcass cooling and oxygen consumption of Sorex cinereus trapped near Fairbanks, Alaska in February and March. They found a value of $0.31 \text{ cal/cm}^2/\text{hr}/^\circ\text{C}$ for an extended carcass, $0.53 \text{ cal/cm}^2/\text{hr}/^\circ\text{C}$ for a curled carcass, and $0.59 \text{ cal/cm}^2/\text{hr}/^\circ\text{C}$ in living Sorex by measurement of oxygen consumption. The differences in heat loss in Blarina between summer and winter-caught shrews as measured by carcass cooling and as measured by oxygen consumption indicate that the increased insulation partially accounts for the reduced metabolism in winter-caught shrews. Compared to summer-caught shrews under the same conditions, winter-caught shrews had a 63.05% lower heat loss as estimated from metabolic heat production for all activity levels. Heat loss from winter-caught carcasses was 21.64% lower than from summer-caught shrew carcasses (Table 13).

Thermal Balance

Although attempts were made to assess the primary components of heat transfer as accurately as possible, several factors in the design of the Thermal Balance experiment should be considered. (1) Changes in the partial pressure of oxygen in the metabolism chamber outlet airstream may lag behind the ambient air temperature changes even though the measurements were sequenced to minimize this problem. (2) Estimates of metabolism were made using oxygen consumption data including all activity levels. (3) Surface temperature of the shrew was measured in only one location and assumed to be uniform over the entire body surface. (4) A constant surface area was assumed for all shrews. (5) Water loss was not measured directly; the estimates of water loss were based on data of Chew (1951). (6) The change in metabolism chamber wall temperature occasionally would lag slightly behind the change in the ambient air temperature. (7) Estimates of radiation absorbed by the shrew were based on radiometer measurements of thermal energy flux in the environmental cabinet. (8) The radiometer was located near but external to the metabolism chamber. (9) The metabolism chamber was constructed of plexiglas (polymethyl methacrylate) which is approximately 100% transmissive to wavelengths up to one micron. For wavelengths from one micron to 2.8 microns transmissivity varies from 0% to peaks of 70% and 90%; above 2.8 microns transmissivity is 0%.

Under the conditions of the Thermal Balance experiment, the thermal balance model is used to predict metabolic rates for selected levels of incoming radiation. The model predicts a metabolic rate of $0.122 \text{ cal/cm}^2/\text{min}$ (512 cal/hr) for a summer shrew with a radiation environment of $0.415 \text{ cal/cm}^2/\text{min}$. The temperature equivalent is 20° C if the thermal radiation is all long-wave infrared energy. In the Thermal Balance experiment at 20° C and a radiation environment of $0.385 \text{ cal/cm}^2/\text{min}$, the mean metabolic rate of summer-caught shrews at activity level 2 was 425 cal/hr .

High levels of locomotor activity in a high radiation environment could result in an increase in body temperature unless thermoregulatory action is taken by the animal. Heat loss by respiratory exchange could be used, but this may result in water balance problems. A summer shrew with a metabolic rate of $0.221 \text{ cal/cm}^2/\text{min}$ (929 cal/hr) in a radiation environment of $0.415 \text{ cal/cm}^2/\text{min}$ would require a water loss of approximately 0.75 cc/hr to re-establish thermal balance by evaporative cooling. Chew (1951) measured an insensible water loss of $0.08 \text{ cc/cm}^2/\text{day}$ for Blarina at 24° C . The equivalent water loss for a shrew with a surface area of 70 cm^2 at a normal, exploring metabolic rate would be about 0.23 cc/hr . Pearson (1947) suggests that Blarina brevicauda and Sorex cinereus could not withstand temperatures higher than 27° C for long periods. Using their own model, Porter and Gates (1969) predict

that Sorex cinereus could not withstand a still air temperature greater than 24° C for any length of time, primarily because of water loss. The combination of high metabolic rates and water loss rates may restrict Blarina to cool, moist habitats. Pruitt (1953, 1959) and Getz (1961) found that Blarina normally inhabits cool, moist areas.

The model predicts that a winter shrew would be in thermal balance by maintaining a metabolic rate of 0.142 cal/cm²/min (598 cal/hr) if the radiation environment were 0.258 cal/cm²/min (Table 14). The temperature equivalent is 0° C, if the thermal radiation is all long-wave infrared energy. In the Thermal Balance experiment at 0° C and a radiation environment of 0.239 cal/cm²/min, the mean metabolic rate of winter-caught shrews at activity level 2 was 600 cal/hr.

High levels of locomotor activity in a low radiation environment could be beneficial in thermoregulation. If a winter shrew maintained a metabolic rate of 0.195 cal/cm²/min (818 cal/hr), thermal balance could occur in a radiation environment of 0.102 cal/cm²/min or a temperature equivalent to -20° C (Table 14). Metabolic rates of 900 cal/hr were attained during hyperactivity of winter-caught shrews at 3° C in the Locomotor Activity Costs experiment.

TABLE 14
 PREDICTED BLARINA METABOLISMS FOR
 THREE THERMAL RADIATION ENVIRONMENTS

<hr/>			
If Thermal Radiation Environment is			
cal/cm ² /min	0.415	0.258	0.102
Equivalent Temperature °C	+20	0	-20
<hr/>			
Winter Shrew Metabolism at $H_g = H_1$ is			
cc O ₂ /gm/hr	5.20	6.16	8.43
cal/cm ² /min	0.120	0.142	0.195
cal/animal/hr	505	598	818
<hr/>			
Summer Shrew Metabolism at $H_g = H_1$ is			
cc O ₂ /gm/hr	5.27	6.30	8.63
cal/cm ² /min	0.122	0.146	0.199
cal/animal/hr	512	612	837
<hr/>			

Predator-Prey System

Examples of the output from the submodel of the thermal balance of an individual predator are in Figure 19. All estimates were calculated using the temperature at the soil:leaf litter interface. Summer temperatures as a function of time in hours are expressed graphically in Figure 17. Under winter conditions, the soil:leaf litter interface temperature was 0° C.

In its natural habitat the shrew may receive several streams of radiation of various intensities and spectral compositions. The shrew presents various areas to the different incident fluxes of radiation. In this submodel the estimates of the thermal energy gain by absorption (Q) assume that the shrew is exposed to the same radiation flux equally over the entire body surface. The estimates of the thermal energy loss by radiation (R) utilize the regressions of Δt (fur surface temperature - ambient air temperature) on ambient temperature, as seen in Figure 13. The thermal energy loss by convection (C) and the thermal energy loss by evaporation (E) are also estimated using the soil:leaf litter interface temperatures. The estimates of thermal energy production by metabolism are based on the regressions of metabolic rate (M_a) at a constant ambient temperature as a function of locomotor activity level (Figure 8) and the regressions of metabolic rate (M_t) at the same locomotor activity level as a function

FIG. 19 a. Primary components of heat transfer as estimated with the model of thermal balance of an individual summer shrew under summer field conditions. R is radiation loss, Q is radiation absorbed, and M is metabolism. $\bar{M}$ is the mean of the hourly metabolic rates M. Net heat exchange (N) is total heat gain ($H_g = M + Q$) less total heat loss ($H_l = R + C + E$). $\bar{N}$ is mean net heat exchange, where total heat gain is $\bar{H}_g = \bar{M} + Q$ and total heat loss is $H_l = R + C + E$. All units are cal/animal/hr, for a 20 gm, 70 cm² shrew.

FIG. 19 b. Primary components of heat transfer as estimated with the model of thermal balance of an individual winter shrew under winter field conditions. Other details listed above are also true for this case.

of ambient temperature (Figure 12). Locomotor activity level is expressed as a function of time in hours in Figure 18. Total metabolism (M) for the medium locomotor activity distribution ($c = 0.6$) is expressed as a function of time for both summer shrews under summer conditions and winter shrews under winter conditions in Figure 19.

Unlike the Thermal Balance experiment in which conditions were standardized and direct measurements were made in order to calculate M, Q_{abs} , and $\epsilon\sigma T_r^4$, the values of M, Q, and R calculated with the individual thermal balance submodel are estimates, based on laboratory data and temperatures measured in shrew habitat. Clearly this is a highly simplified approach but this submodel was intended to be more general and less precise. For example, as seen in Figure 19, the thermal heat loss by radiation (R) curve does not reflect the changes in metabolism (M) due to the bimodal locomotor activity distribution.

Net heat exchange (N) is total heat gain ($H_g = M + Q$) less total heat loss ($H_l = R + C + E$). For both summer and winter conditions, when metabolic rates (M) are high the net heat exchanges (N) are positive; at low metabolic rates the net heat exchanges are negative. $\bar{M}$ is the mean of the hourly metabolic rates M. $\bar{N}$ is mean net heat exchange, where total heat gain is $\bar{H}_g = \bar{M} + Q$ and total heat loss is $H_l = R + C + E$. During summer conditions the shrew's mean net heat exchange is slightly

negative. During winter conditions the shrew's mean net heat exchange is slightly positive. Although the mean net heat exchanges ($\bar{N}$) are not at zero (which indicates a thermal steady-state), values of $\bar{H}_g$ and H_l are less than 5% different under both seasonal conditions.

The estimates of R and Q were not used in the calculations of the total daily metabolism of an individual shrew. Total daily metabolism was calculated by integration of the hourly metabolic rates (M). However integration of M and of $\bar{M}$ through the 24 hr period does result in the same value for total daily metabolism. Using the medium daily activity level (Figure 18) an individual shrew's total daily metabolism is estimated to be 11.180 kcal under summer conditions and 16.019 kcal under winter conditions.

Table 15 is a comparison of the amount of prey energy required for an individual shrew at three different daily activity levels, both during summer and winter, as estimated with the model. Season has a more pronounced effect on a shrew's prey energy requirement than does the daily level of locomotor activity. At low activity levels the daily energy requirement under winter conditions is 58.45% higher than at the same activity level under summer conditions. At the medium activity level the daily energy requirement under winter conditions is 42.90% higher than at the same activity level under summer conditions. This difference decreases to 37.32% at the high daily activity level.

TABLE 15
DAILY FOOD ENERGY REQUIREMENT^a OF AN INDIVIDUAL BLARINA

Season	Daily Activity ^b				% ($\frac{H-L}{H}$)
	High (.8)	Med (.6)	Low (.2)	H - L	
Winter	23.40	22.15	19.67	3.73	18.96
Summer	17.04	15.50	12.42	4.62	37.19
W - S	6.36	6.65	7.25	-	-
% ($\frac{W-S}{S}$)	37.32	42.90	58.45	-	-

^a Units are cal/animal/day.

^b From Figure 18.

In the Manotick woodlot the prey populations have a high level of locomotor activity during a 182-day summer season and are typically inactive during a 182-day winter season. Due to prey activity, reproduction, and life cycle changes, the same area of the forest floor may have a sustained low-level yield of prey energy throughout the entire summer season. In contrast most of the prey energy eaten by a predator in an area of the forest floor during the winter will not be replaced for the duration of the season. The prey energy available per square meter of forest floor for the 182-day summer season is estimated to be about 8 times the prey energy available per square meter for the 182-day winter season. For the 2.618 hectares (6.47 acres) of the Manotick woodlot the total prey energy base (PEB) is estimated at 219×10^6 calories for the 182-day winter season and 1779×10^6 calories for the 182-day summer season.

Blair (1941) and Buckner (1966) estimate that Blarina lives at densities of 0.5 to 2 individuals per acre. Using the higher density, the 6.47 acre Manotick woodlot would be expected to have a Blarina population of 13. An expected population size of 20 and a high population size of 50 were used in the model. Table 16 is a summary of metabolism, production, and prey requirements for these two population sizes, as have been determined with the model.

Total energy utilization is the population metabolism plus the population production. About 1% of the

TABLE 16

SEASONAL SUMMARY OF BLARINA POPULATION ENERGETICS

Energy in calories x 10 ⁶ per season	Population Size			
	20		50	
	Season			
	Summer	Winter	Summer	Winter
Metabolism	40.7	58.3	101.8	145.8
Production	0.6	0.6	1.3	1.3
Prey Energy Base	1779	219	1779	219
Prey Energy Used	56.5	80.7	141.2	202.1
Prey Used/Prey Base	.03	.37	.08	.92

total energy utilization of the Blarina populations went into production. Odum, Connell, and Davenport (1962) found that about 2% of the total energy utilization of Peromyscus polionotus went into production. According to Golley (1960), production accounts for about 3% of the total energy utilization of Microtus pennsylvanicus populations. Although a number of assumptions were required to make an estimate of individual Blarina productivity, estimates of population production appear comparable to those found in two other small mammal populations.

A population of 20 Blarina in the Manotick woodlot would require only about 3% of the total prey energy base during the summer and about 37% of the prey energy base during the winter. The annual energy flow (utilization) through this population would be $3.86 \text{ kcal/m}^2/\text{year}$. The average energy flow for a population of Peromyscus polionotus in an old-field ecosystem in Georgia was estimated to be $6.7 \text{ kcal/m}^2/\text{year}$ (Odum, Connell, and Davenport, 1962).

A Blarina population of 20 adult individuals in the Manotick woodlot should experience little difficulty in obtaining sufficient food both during summer and winter. The maximum Blarina population that might be supported by the Manotick woodlot is about 50 individuals. This number is unlikely since there would be a density of 7.7 shrews per acre and these 50 individuals would require 92% of their prey energy base during the winter.

APPENDICES

- I. CALORIC EQUIVALENTS OF ORGANISMS
COLLECTED IN THE SUMMER**
- II. CALORIC EQUIVALENTS OF ORGANISMS
COLLECTED IN THE WINTER**
- III. FORTRAN PROGRAM OF MODEL**

CALORIC EQUIVALENTS OF ORGANISMS COLLECTED IN THE SUMMER

Organism	Sample Size (no)	Dry Weight (gm)	Caloric Equivalent (cal/gm) ^a
<u>Carabus</u>	20	2.1862	5777.6
<u>Pterostichus</u>	30	1.6558	5739.2
<u>Calathus</u>	10	0.1628	5484.6
<u>Ceuthophilus</u>	25	2.0722	5522.4
Julida	65	0.4614	4002.0
Polydesmida	2	0.0280	4074.3
Lycosidae	7	0.1680	5532.6
Other Araneae	19	.1461	5176.5
Annelida	3	0.1028	5223.4
<u>Bufo</u>	1	0.2008	5181.4
<u>Sorex</u>	1	0.7644	5689.6
<u>Blarina</u>	1	6.8322	5876.3
<u>Peromyscus</u>	1	4.0192	5520.3
<u>Clethrionomys</u>	1	3.5572	5852.1

^aCaloric equivalent is calories per ash-free, freeze-dried gram.

CALORIC EQUIVALENTS OF ORGANISMS COLLECTED IN THE WINTER

Organism	Sample Size (no)	Dry Weight (gm)	Caloric Equivalent (cal/gm) ^a
<u>Acrosternum</u>	42	1.1826	5873.6
<u>Vespula</u>	2	0.1618	5505.2
<u>Mesodon</u> ^b	27	0.7366	3585.1
Julida	66	0.7427	4577.3
Lycosidae	8	0.2113	5577.0
Henicopidae	66	0.1564	6322.9
Elateridae larvae	94	0.7851	6184.9
Tipulidae larvae	42	0.5030	5351.6
Lepidoptera larva	1	0.0469	6002.6
Carabidae larvae	17	0.1177	4592.2
Noctuidae pupa	1	0.2266	5811.8
Annelida	40	1.4000	5531.4

^aCaloric equivalent is calories per ash-free, freeze-dried gram.

^bIncludes calcareous shells.

FORTRAN PROGRAM OF MODEL

```

      DIMENSION TCYCLE(24),TEMP(24),ACYCLE(24),ASIN(24),
      IACTLEV(24),TMR(24),AMR(24),GABS(24),CCW(24),VAPOR(24),
      IESW(24),DELTF(24),FURSUR(24),CONCO(24),CONVEC(24),
      IRAD(24),GAIN(24),LOSS(24),BAL(24)
      INTEGER HOUR,S
      REAL METAB,LOSS
      PRINT 10
10  FORMAT ('SELECT SEASON: SUMMER = 1, WINTER = 2 ; IN I1')
      READ 20,S
20  FORMAT (I1)
      IF (S.EQ. 2) GO TO 21
      SV1 = 3.0
      SV2 = 18.0
      SV3 = 544.86
      SV4 = 20.37
      SV5 = 16.33
      SV6 = 126.30
      SV7 = .6616
      SV8 = -.0349
      SV9 = 16.3242
      SV10 = 432000000.
      GO TO 22
21  SV1 = 0
      SV2 = 0
      SV3 = 583.83
      SV4 = 7.53
      SV5 = 13.68
      SV6 = 101.60
      SV7 = .6103
      SV8 = -.0291
      SV9 = 13.6764
      SV10 = 219000000.
22  CONTINUE
      PRINT 40
40  FORMAT ('INPUT ELARINA POPN SIZE IN F3.0 FORMAT')
      READ 50,POP
50  FORMAT (F3.0)
      PRINT 60
60  FORMAT ('INPUT ELARINA PRODUCTIVITY (CAL/DAY) IN F5.1')
      READ 70,PROD
70  FORMAT (F5.1)
      PRINT 80
80  FORMAT ('SET ACTIVITY LEVEL: HI=.8,MED=.5,LO=-.2; INPUT F2.1')

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READ 90, ACTSET
90  FORMAT (F2.1)
PRINT 100
100  FORMAT ('CHANGE TEMP BASE BY +/-? DEG IN F2.0')
READ 110, TDELTA
110  FORMAT (F2.0)
PRINT 120
120  FORMAT ('TIME IN DAYS?; INPUT IN I3')
READ 130, N
130  FORMAT (I3)
METAB = 0
DO 2 HOUR = 1, 24, 1
  TCYCLE(HOUR) = SV1 * COS(3.6127 + (2.1991 * HOUR) / 12.0)
  TSET = SV2
  TEMP(HOUR) = TSET + TCYCLE(HOUR) + TDELTA
  ACYCLE(HOUR) = ABS((.2618 * HOUR) - 3.1416)
  ASIN(HOUR) = ABS(SIN(ACYCLE(HOUR)))
  ACTLEV(HOUR) = 1. + (((.2 * ACYCLE(HOUR)) +
1 (ACTSET * (ACYCLE(HOUR) ** 2.))) * ASIN(HOUR)
  TMR(HOUR) = SV3 - SV4 * (TEMP(HOUR) - SV5)
  AMR(HOUR) = TMR(HOUR) + SV6 * (ACTLEV(HOUR) - 2.5)
  METAB = METAB + AMR(HOUR)
  QABS(HOUR) = (.4443 + (9.0698E-3) * (TEMP(HOUR) - 16.)) * 3360.
  CCW(HOUR) = (.01 + .0015 * (TEMP(HOUR))) / 1440.
  VAPOR(HOUR) = 595.90 - .56 * (TEMP(HOUR))
  ESW(HOUR) = (CCW(HOUR) * VAPOR(HOUR)) * 4200.
  IF (ESW(HOUR) .LT. 0) ESW(HOUR) = 0
  DELTF(HOUR) = SV7 + SV8 * (TEMP(HOUR) - SV9)
  FURSUR(HOUR) = TEMP(HOUR) + DELTF(HOUR)
  CONVEC(HOUR) = ((9.057E-3) * DELTF(HOUR)) * 4200.
  RAD(HOUR) = ((.8) * (.817E-10) * (FURSUR(HOUR) + 273.)) ** 4. * 4200.

  GAIN(HOUR) = QABS(HOUR) + AMR(HOUR)
  LOSS(HOUR) = RAD(HOUR) + CONVEC(HOUR) + ESW(HOUR)
  BAL(HOUR) = GAIN(HOUR) - LOSS(HOUR)
2  CONTINUE
  UFOOD = METAB / .80
  FECES = UFOOD - METAB
  DFOOD = UFOOD + PROD
  HLOSS = .10 * UFOOD
  FREQ = DFOOD + HLOSS
  POPMET = POP * METAB * N
  POPCHW = POP * FECES * N
  POPPROD = POP * PROD * N
  PREY = POP * FREQ * N
  GATE = PREY / SV10
  RPREY = POPMET / PREY
  INDIV = POPPROD / 35250.
PRINT 140
140  FORMAT (///, 6X, 'DAILY THERMAL ENERGY BALANCE')
PRINT 150
150  FORMAT (///, 6X, 'TIME', 6X, 'TEMP', 6X, 'ACT', 8X, 'METAB',
18X, 'QABS', 8X, 'RAD')
DO 4 HOUR = 1, 24, 1
  PRINT 160, HOUR, TEMP(HOUR), ACTLEV(HOUR), AMR(HOUR),
1 QABS(HOUR), RAD(HOUR)
160  FORMAT (7X, I2, 8X, I2, 8X, F3.1, 8X, F6.1, 7X, F6.1, 6X, F6.1)

```



```

4  CONTINUE
   PRINT 170
170  FORMAT (//, 6X, 'TIME', 7X, 'CONV', 8X, 'ESW', 9X, 'GAIN',
        18X, 'LOSS', 8X, 'BAL')
      DO 5 HOUR = 1, 24, 1
      PRINT 180, HOUR, CONVEC(HOUR), ESW(HOUR), GAIN(HOUR),
        1LOSS(HOUR), BAL(HOUR)
180  FORMAT (7X, I2, 7X, F6.1, 7X, F6.1, 6X, F6.1, 6X, F6.1, 6X, F6.1)
5  CONTINUE
   PRINT 185, ACTSET
185  FORMAT (//, 3X, 'DAILY ACTIVITY DISTRIBUTION = ', 2X, F3.1)
   PRINT 190
190  FORMAT (////, 6X, 'DAILY CHEMICAL ENERGY BALANCE')
   PRINT 200, METAB
200  FORMAT (//, 3X, 'METABOLIZABLE ENERGY = ', 6X, F10.2)
   PRINT 210, UFOOD
210  FORMAT (/, 3X, 'INGESTED ENERGY = ', 11X, F10.2)
   PRINT 220, FECES
220  FORMAT (/, 3X, 'FECAL & URINARY LOSS = ', 6X, F10.2)
   PRINT 230, HLOSS
230  FORMAT (/, 3X, 'HANDLING LOSS = ', 13X, F10.2)
   PRINT 240, PROD
240  FORMAT (/, 3X, 'PRODUCTIVITY = ', 14X, F10.2)
   PRINT 250, FREQ
250  FORMAT (/, 3X, 'PREY ENERGY REQUIRED = ', 6X, F10.1)
   PRINT 260
260  FORMAT (///, 12X, 'SEASONAL SUMMARY')
      IF (S.EQ.2) GO TO 6
   PRINT 270
270  FORMAT (//, 18X, 'SUMMER')
      GO TO 7
6  PRINT 280
280  FORMAT (//, 18X, 'WINTER')
7  PRINT 290, N
290  FORMAT (//, 3X, 'TIME IN DAYS = ', 20X, I3)
   PRINT 300, POP
300  FORMAT (/, 3X, 'BLARINA POPULATION SIZE = ', 8X, I5)
   PRINT 310, POPMET
310  FORMAT (/, 3X, 'POPULATION METABOLISM = ', 10X, E10.3)
   PRINT 320, POPROD
320  FORMAT (/, 3X, 'POPULATION GROWTH = ', 15X, E10.3)
   PRINT 330, INDIV
330  FORMAT (/, 3X, 'EQUIVALENT INDIVIDUALS = ', 10X, I4)
   PRINT 340, SV10
340  FORMAT (/, 3X, 'PREY RESOURCE BASE = ', 14X, E10.3)
   PRINT 350, PREY
350  FORMAT (/, 3X, 'PREY RESOURCE USED = ', 14X, E10.3)
   PRINT 360, GATE
360  FORMAT (/, 3X, 'PREY USED / PREY AVAILABLE = ', 5X, F5.2)
   PRINT 370, RPREY
370  FORMAT (/, 3X, 'POPULATION METABOLISM / PREY USED = ', 5X, F5.2)

8  END

```

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Department of Biology and Ontario Department of University Affairs grants to Dr. H.G. Merriam and from a National Research Council grant to Dr. C.A. Barlow.

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