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THE WINTER ECOLOGY AND BIOENERGETICS OF THE OPOSSUM, DIDELPHIS MARSUPIALIS, AS DISTRIBUTIONAL FACTORS IN MICHIGAN

By

Rainer Hans Brocke

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ABSTRACT

THE WINTER ECOLOGY AND BIOENERGETICS
OF THE OPOSSUM, DIDELPHIS MARSUPIALIS,
AS DISTRIBUTIONAL FACTORS
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Rainer Hans Brocke

The opossum's recent northward population expansion in North America suggests that it possesses effective adaptations to temperate winter cold. Interrelationships of the opossum's anatomy, physiology, behavior and environment were studied in southern Michigan during winter. Field observations, electrically monitored activity of penned opossums and data from 154 road-killed opossums collected throughout southern Michigan indicate that opossums leave their dens to forage in winter on those days when the air temperature exceeds the freezing point. Almost all foraging activity ceases at air temperatures below -5°C. Snow appears to affect opossums primarily by covering the food supply and hindering travel. Opossums use ground dens in winter dug by other mammals. Between December 1, 1967, and March 29, 1968, the lowest daily mean temperature for six artificial ground den cavities in outdoor pens holding opossums was 0.6°C (of 1440 measurements, 1 m below ground surface), while the lowest recorded temperature for air was

$-22.8^{o}C$. The mean winter air temperature fluctuation for the 24 hour period was $9.9^{o}C$. For ground den cavities, it was $0.3^{o}C$. Thermal characteristics of eight natural dens paralleled those of artificial dens. With the approach of spring and warm weather, penned opossums gained a thermal advantage as they occupied artificial tree dens more frequently than ground dens. Analysis of stomach contents of 20 road-killed specimens showed animal remains in 85% of all stomachs. The resting body temperature (T_B) of five acclimatized opossums declined with declining air temperature (T_A), according to the regression: $T_B(C^o) = 33.65 + 0.048T_A$. Oxygen consumption of four opossums (mean weight 3.48kg) is given by the equation: RMR (ml O_2/g/hr) = $0.51 - 0.014\ T_A(C^o)$. The BMR calculated from the equation is 0.15 ml O_2/g/hr or .72 kcal/kg/hr, among the lowest of rates for mammals. Winter energy requirements of opossums confined in outdcor pens with artificial tree and ground dens was determined by food balance calorimetry. The mean metabolizable energy (ME) derived from ad libitum daily ingestion of whole rabbit is 131 kcal/kg body wt./day (four opossums, 43 trials). The mean ME expenditure of seven opossums in artificial ground dens (for minimum activity and sleep at T_{AS} just above freezing) is 1.96 kcal/kg/hr. The mean ME expenditure of eight opossums (mean weight 2.25 kg) at higher activity levels is 2.92 kcal/kg/hr. The mean ME equivalent of body weight loss for seven opossums is

4.38 kcal/g weight lost. Approximately one-third of the opossum's winter energy expenditure is provided by catabolism of body substance, and two-thirds by food. The body fat fraction of road-killed opossums was calculated from specific gravity determinations of eviscerated carcasses. Decline in body fat of 54 opossums related to days of the winter period (December 1 = Day 1; March 29 = Day 120), is described by the regression: $Y = 27.13 - 0.157\ X$; where Y represents the lipid fraction of body weight in percent, and X represents days of the winter period. Likewise, winter decline in body weight of 138 road-killed opossums is described by the regression: $Y = 3012.4 - 7.67\ X$; where Y represents body weight (g) and X represents days of the winter period. One gram of body weight supplies 5.03 kcal of ME according to fat and weight decline data. Maximum weight losses of penned animals over the winter period ranged from 40 to 45%. Three mathematical models of winter survival were calculated for a theoretical winter period of 120 days. The number of enforced winter sleep days (days with sub-freezing temperatures) determines how many potential foraging days remain in the 120 day winter period. The mandatory energy intake (energy deficit) per foraging day increases northward as the potential number of foraging days decreases. Assuming complete foraging success (315 kcal per foraging day) opossums can theoretically survive 90 days of enforced winter sleep if 30 foraging days with complete

foraging success are available. Presently, the northern distributional limit of the opossum in Michigan coincides with a winter severity level of 70 enforced days of sleep, or the approximate southern limit of the pine-hemlock ecotone region. Limitations of deep snow on distribution are discussed. The hypothesis is presented that winter energy limitations will generally restrict opossum populations in northeastern North America to points south of this ecotonal boundary. Perhaps the opossum's physiological-behavioral response to winter is unique among temperate mammals because potential generalized ecological niches to accommodate its low-key mode of life are restricted.

"There are wood rats here as big as a French cat, which have white fur---. The female has two skins under her belly which gives the effect of a cloak closed at the top and bottom and open in the middle. They have as many as eight young, which they carry inside when they walk. Some savages brought me a couple once during the winter. I hoped to send them to France, but I was surprised some days afterward to find their tails missing. The cold had frozen them and they had broken off like glass. Sometime later their ears also dropped off, so that I was obliged to kill them. Some savages to whom I told this informed me that the mothers always kept them in their holes until they were as big as themselves, and that they never went out when it was very cold."

Memoir of Pierre Liette (a French army officer) concerning the Illinois country, 1702, from "The Western Country in the 17th Century", by M. Quaife (ed), quote courtesy of the Citadel Press.

To my families
the Brockes and Biebesheimers

and to

Dr. E. Paul Reineke
Professor of Physiology
Michigan State University

ACKNOWLEDGMENTS

For their guidance and generous assistance in this research project, I express my sincere thanks and deep appreciation to my major professor, Leslie W. Gysel, and to members of my doctorate committee, Professors E. Paul Reineke, Duane E. Ullrey, Manfred D. Engelmann and Rollin H. Baker. I am grateful to personnel of the Michigan Department of Natural Resources who collected specimens for this study, particularly to Ralph I. Blouch and C. T. Black. This research was supported by the Michigan Agricultural Experiment Station, in part through a Graduate Research Assistantship for the winter of 1968. I appreciate the financial support accorded by the faculty position I held for five years in the Department of Natural Science. Finally, I am deeply grateful to my wife, Mary, for her patience and encouragement.

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CHAPTER I

INTRODUCTION

The opossum seems strangely out of place in the temperate winter environment as it wallows through the snow with bare, frost-bitten appendages. Yet this primitive marsupial has shown itself to be eminently adapted to cold, competing successfully with more highly evolved placental mammals. Within recent history, it has affected a remarkable northward expansion of its range in North America (Seton 1909, Goodwin 1935, Peterson and Downing 1956, Hamilton 1958, Guilday 1958 and others). In the eastern and central portions of the continent, population expansion followed the clearing of primeval forest. Michigan was first occupied by the opossum around 1845 (Wood and Dice 1923). It is presently common in the southern half of the Lower Penninsula.

The opossum's ecological success in the north poses several intriguing questions: What are its adaptations to winter cold? How are its winter ecology and physiology related? In which ways does it interact and compete with other species? How does winter severity affect its distribution? What possible ecological explanation can account for its recent northward range expansion? The purpose of this study was to seek answers to these questions by investigating pertinent interrelationships of the opossum's anatomy, physiology, behavior and environment during the season of greatest stress, the winter. Emphasis has been placed on winter bioenergetics as this is apparently the most critical aspect of opossum survival in temperate North America. Michigan is uniquely qualified as a study area. The present northern boundary of the opossum's range approximately bisects the state and has remained relatively stable for the last 40 years (Taube 1942 and present study). This fact has greatly facilitated determination of ecological energy limitations.

There is a paucity of physiological-ecological data on the North American opossum. Previous ecology-related studies have dealt primarily with the opossum's natural history, foods and distribution (Dearborn 1932, Lay 1942, Taube 1942, Reynolds 1945, Wiseman and Hendrickson 1950, Fitch and Sandidge 1953, and Hamilton 1958). Most physiological data have been obtained under laboratory conditions (Brown 1909, Johnson 1931, Wislocki 1933, Scott 1938, Higginbotham and Koon 1955, Petajan and Morrison 1962, and Francq 1967). A concerted effort has been made here to seek physiological measurements and make interpretations in the context of the natural environment. Hart (1957) commenting on investigations to determine the adjustment of animals to "heat" and "cold" indicates differences between the laboratory and natural environments as follows: (1) In the laboratory, experimental animals are exposed to constant and continuous temperatures instead of fluctuating temperatures as found in the normal habitat. (2) Animals are not subjected to other environmental factors that may play an important role in nature. In his thorough review of homeotherm energetics, Hart compares data for climatic and temperature induced changes. For example, in the laboratory, animals acclimated to cold raise heat production at any given temperature and reduce overall insulation through greater peripheral heating. In contrast, animals acclimatized to winter conditions either show no change in heat production at any given temperature or show a lower heat production with increased overall insulation. Obviously, physiological data have to be interpreted and used with care by the ecologist. In the present study, data were obtained from fully acclimatized animals subjected to normally encountered thermal stresses (East Lansing, Michigan).

Ecological bioenergetics studies usually tend to have either a synecological or autecological emphasis. Investigations in the former category are concerned with energy flow through whole natural communities. Notable studies of this type are by Lindeman (1942), Golley (1960), Engelmann (1961), Odum et al (1962), Golley and Gentry (1964), Wiegert (1964) and Petrides and Swank (1965). The autecological approach, used in the present study, stresses species energetics related to various key environmental factors operating over a daily, seasonal or annual span of time. A primary objective in this type of study is to define possible energy limitations imposed on an organism by factors of its ecological niche. Such factors are temperature, photoperiod, food, shelter, and interactions with other animals. For want of descriptive terminology, I shall call this the "species-niche energetics" approach. Other studies with the species-niche energetics emphasis are by Kendeigh (1949), Pearson (1960), West (1960), McNab (1963), Zimmerman (1965), McNab (1966), Tucker (1966), Novakowski (1967) and Moen (1968).

CHAPTER II

METHODS AND MATERIALS

Data on oxygen consumption and thermoregulation were collected in the winter of 1965-1966 and during the spring and summer of 1966. Most other data were obtained during the winter of 1967-1968 and spring and autumn of 1968. A few field observations included here were made during the winter of 1968-1969.

Standard procedures for statistical analysis were employed (Snedecor 1956).

Study Areas

The extensive portion of this investigation i.e. the collection of specimens was carried out over most of Michigan's Lower Penninsula. Variety is a characteristic of Michigan's climate, geology, soils and vegetation. The southern half of the Lower Penninsula is on the northern fringe of the temperate deciduous forest region (Shelford 1963) with brown forest soils (Veatch 1953). Most of the state's agriculture, industry, people and opossums are located here. The region north of the mid-point of the Lower Penninsula is one of transition between deciduous forest and boreal coniferous forest (Shelford 1963). This so-called "Great Lakes Forest" region has podzolic soils of low fertility, covered by second growth deciduous and coniferous forest, a legacy of intensive logging. Winters are more severe here, and opossums largely absent. Pertinent climatic and ecological data will be presented farther in the text. For a detailed description of the geology, soils and vegetation of Michigan, the reader is referred to the classic work of Veatch (1953).

Intensive field observations were made on two tracts of land located seven miles apart, east of the Michigan State University campus at East Lansing. The combined area of these tracts is one half of a square mile. Experimental pens were located on one of these tracts (Area I). The other tract is a portion of the Rose Lake Wildlife Experiment Station of the Michigan Department of Natural Resources (Area II). Both areas consist of abandoned farmland, primarily of sandy loam soils. A small stream runs through each of these tracts.

The vegetation is quite variable. The combined percentage of cover types is as follows: Ploughed field 2%, grassland and scattered shrubs 42%, sedge and cattail marsh 5%, dense shrub stands 14% (primarily dogwoods, sumac and prickley ash), second growth hardwoods 8% (primarily aspen, black oak, cherry and elm). Some of these cover types are illustrated in Figures 38, 39 and 40 in Appendix B. Both tracts harbored a variety of wildlife, including white-tailed deer.

Field Observations

Movements and foraging behavior of wild opossums were followed closely on both study areas, primarily by tracking in the snow. In some cases it was possible to keep continuous activity records of individual animals. Ground dens were visited periodically to record den temperatures. Temperatures were measured with an electrical thermistor-thermometer (Yellow Springs Telethermometer Model 42SF) using a long, semi-flexible probe inserted into the burrow. This instrument was calibrated and periodically checked against a mercury thermometer. It proved to be accurate, although somewhat slow. Air temperature and wind velocity (by anemometer) were recorded with daily field observations. These data were obtained from instruments permanently located near the experimental pens on Area I. Taylor maximum-minimum mercury thermometers and a Bacharach Tempscribe recording thermometer were used to measure air temperature continuously.

Experimental Enclosures and Artificial Dens

Opossums were confined in eight enclosures with artificial dens (Figure 1, and see Figures 32, 33, 34, 35, 36, and 37 in Appendix B), providing quantitative data on:

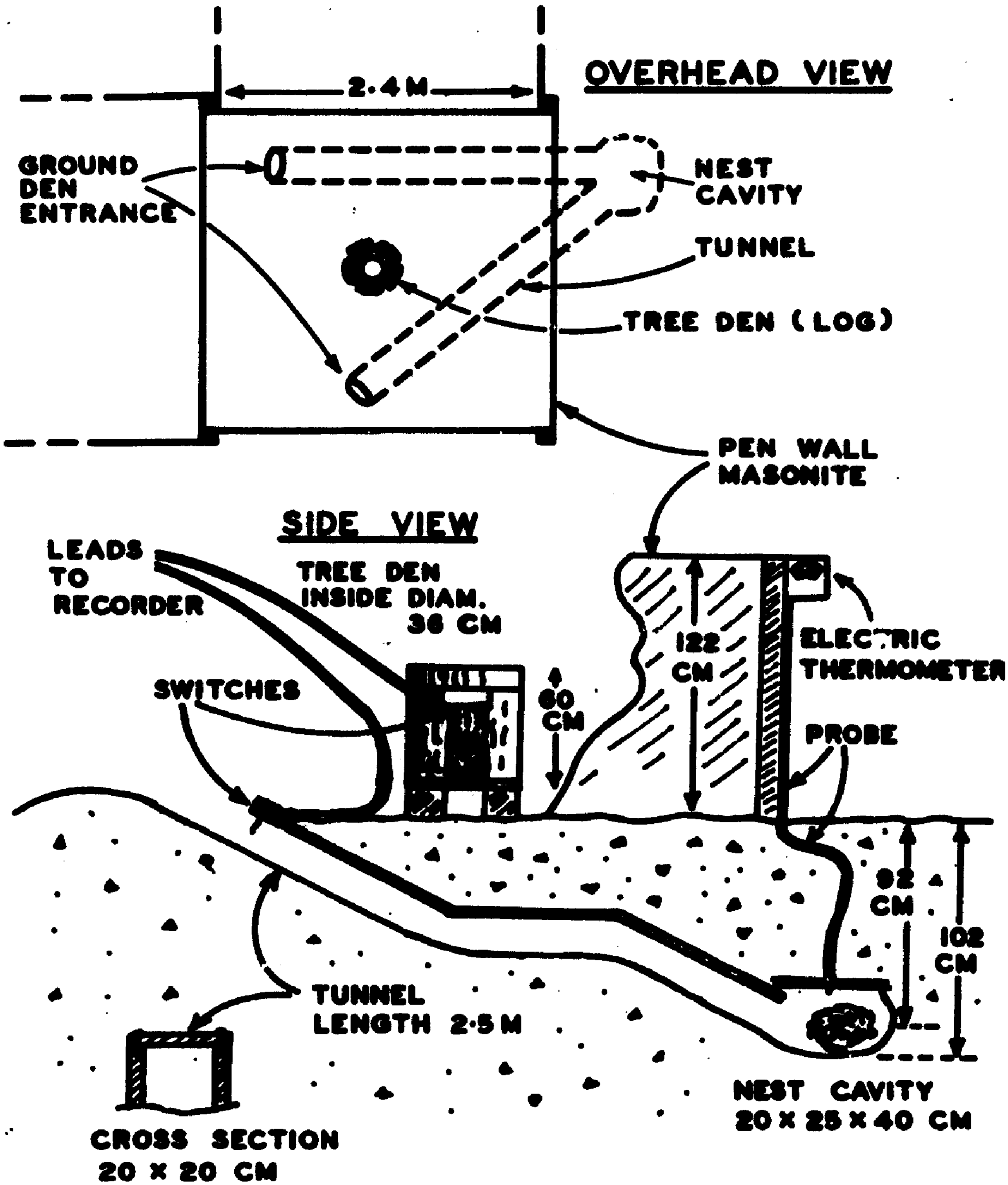
1. Winter behavior.
2. Activity in relation to climatic conditions.
3. Den selection and use. Animals were provided a choice of artificial ground dens or tree cavities.
4. Energy expenditure, under conditions closely approximating those of the natural environment.

Opossums do not dig their own dens but use almost any available ground den of suitable dimensions. Therefore, artificial ground dens were excavated according to the mean dimensions of 36 excavated natural dens in Area II, described by Allen and Shapton (1942). The measurements from ground level to the center and base of each nest cavity were 92 cm and 102 cm respectively (Figure 1). Allen and Shapton's mean maximum depth for 36 natural dens was 100 cm; they report an average of 2.19 openings per natural den. Two tunnels led to the nest cavity in each of the artificial dens. The length of experimental tunnels was shorter than the mean length of natural tunnels due to restrictions imposed by pen size. Tunnels were lined with wood on the upper three sides only, to aid drainage. Nest cavities remained remarkably dry throughout most of the winter. Wood was selected as a lining material because its thermal conductivity is similar to that of sand and clay (Geiger 1966). The soil in the experimental pen area was Hillsdale Sandy Loam, common throughout Areas I and II. Dimensions for tunnels and nest cavities are given in Figure 1.

Artificial tree dens were sections of hollow logs (Figure 1) placed in the center of each pen, 20 cm above the ground. The tree dens were lined with leaves.

The tip of an electric thermometer probe projected into the roof of each of six ground den nest cavities. The cavity temperature was recorded with the telethermometer at least three times daily, at 7:00 a.m., 3:00 p.m. and 10:00 p.m.

Figure 1. Diagram of experimental pens, showing overhead, side and cross-sectional views.


OVERHEAD VIEW
2·4 M
GROUND DEN ENTRANCE
NEST CAVITY
TUNNEL
TREE DEN (LOG)
PEN WALL MASONITE
SIDE VIEW
LEADS TO RECORDER
TREE DEN INSIDE DIAM. 36 CM
SWITCHES
60 CM
122 CM
ELECTRIC THERMOMETER
PROBE
92 CM
102 CM
TUNNEL LENGTH 2·5 M
CROSS SECTION 20 × 20 CM
NEST CAVITY 20 × 25 × 40 CM

Wind velocity and air temperature readings were measured simultaneously with ground den temperatures. At the beginning of the study, it was found that the air temperature in the artificial tree cavities was practically identical with external air temperature. Subsequently, tree cavity temperatures were assumed to equal the measured external air temperature. Probes of two continuous recording thermometers (Bacharach Tempscribe) projected into the nest cavities of the remaining two ground dens. Later, these thermometers were found to be imprecise. Hence, readings of these two dens were not used, except as a general indication of daily temperature trends.

Although all pens and ground dens were constructed according to the same plan, animals were rotated approximately once every 15 days to equalize their exposure to the thermal environment.

An electric switch was placed at every ground and tree den entrance (Figure 1) so that all entries and exits of each animal were recorded. The switch was made of a piece of stainless steel wire insulated by a glass capillary tube, inserted in a short piece of copper tubing (Lawrence and Sherman 1963). The switches were wired to a 20 pen Esterline Angus event recorder. Activity was continuously recorded. At least some activity was recorded for every hour while animals were active. A single switch closing, accomplished by one exit or entry of an animal, was counted as one activity unit. When an animal stood in the entranceway, closing the switch several times in rapid succession, only one activity unit was recorded. The "activity span" was the maximum span of hours in which activity was recorded. Occasionally, activity was not recorded for every hour of the activity span, while animals remained in one location. A quantitative measure of activity intensity was obtained by dividing the total number of recorded activity units per night by the number of hours in the activity span. Recording of opossum activity commenced on February 18, 1968.

Calorimetry by Food Balance

From January 1 to April 3, 1968, winter energy expenditure was measured by food balance calorimetry for opossums confined in the outdoor experimental pens. Energy requirements were determined for a total of seven adult animals and three large juveniles captured prior to, and during the study period. Periods of measurement were 80 days for five animals and ranged from ten to 70 days for the remaining five individuals.

There were two parts to the experimental period, with different objectives. The first part extended from January 1 to February 29. The primary objective during this period was to measure energy expenditure while animals were sustaining an average rate of weight loss of 40% of the initial weight estimated for December 1. The second portion of the experimental period lasted from February 29 to April 3. The primary objective was to determine energy required for maintenance. The body weight of each animal was maintained at its respective level for the duration of this period.

Feeding schedules and associated experimental procedures were necessarily flexible to accommodate unpredictable weather conditions and changing activity patterns of animals. These activity patterns are partly determined by prevailing temperature. Feeding was restricted to nights in which the temperature exceeded -5°C because opossums generally do not leave their ground dens in winter unless the temperature exceeds -5°C. When possible, animals were fed every third day. The frequency of this feeding schedule was adequate to maintain body weight, while minimizing disturbance. This feeding schedule was frequently interrupted during January and February since opossums stayed in their ground dens during cold spells, the longest of which was 14 days. A standard diet of Purina Dog Chow was presented on roofed feeding platforms. All rations were weighed on a triple beam balance with an accuracy of .1gm. As animals were on a maintenance or starvation ration, usually all food was consumed in one or two nights and reweighing of the uneaten remnant was seldom necessary. Water was constantly available, often in the form of ice and snow; opossums will readily eat snow or lick ice to obtain water. Animals were captured by net or box trap prior to each feeding and were weighed on a spring balance to the nearest 10 gms.

A major problem was to decide how much food each animal should have at a particular feeding. An ideal weight curve was constructed for each animal, based on a weight loss rate of 40%, and used as a feeding guideline. Ration size was adjusted upward for any one of the following situations: (1) Whenever the "normal" three day feeding schedule was interrupted by a cold spell. (2) When an animal did not leave the den to feed during a previous three day period even though weather conditions were favorable. This situation occurred occasionally in early winter when fat depots where replete. (3) When nightly activity increased coincident with increasing environmental temperatures in late March.

The metabolizable energy (ME) of the standard winter dog food diet was determined by the total collection method and bomb calorimeter combustion. These measurements were made in September and October 1968. Five adult opossums were seperately confined in metabolism cages 30 x 50 x 200 cm in size for periods of 15 or 21 days (Figures 30 and 31 in Appendix B). A period of adjustment of two weeks or more preceded the measurement period. Animals were held on a maintenance diet of the same dog food used in the experimental winter feeding. Feces and urine collected daily were frozen and stored for caloric analysis. Samples of feces and urine were oven dried at 70° to 80° C and homogenized. Food, feces and urine were combusted in a Parr isothermal jacket bomb calorimeter using standard techniques. As four of the animals yielding ME values were also used in the winter food balance study, their individual ME values were directly applied to calculate their winter energy requirements. The mean ME value for all five animals was applied to all other animals in the winter food balance study.

It was necessary to obtain an estimate of the maximum amount of energy that a wild opossum can ingest in one night. To this end, 43 feeding trials were conducted among four adult opossums. Road-killed cottontail rabbits were fed to these animals ad libitum with water, in April and May. In most cases, these rabbits were completely consumed, including all bone and hair. The combustion value for whcle rabbit was assumed to be the same as that of whole Microtus, or 1.37 kcal/gm wet weight (Golley 1960).

Oxygen Consumption and Temperature Regulation

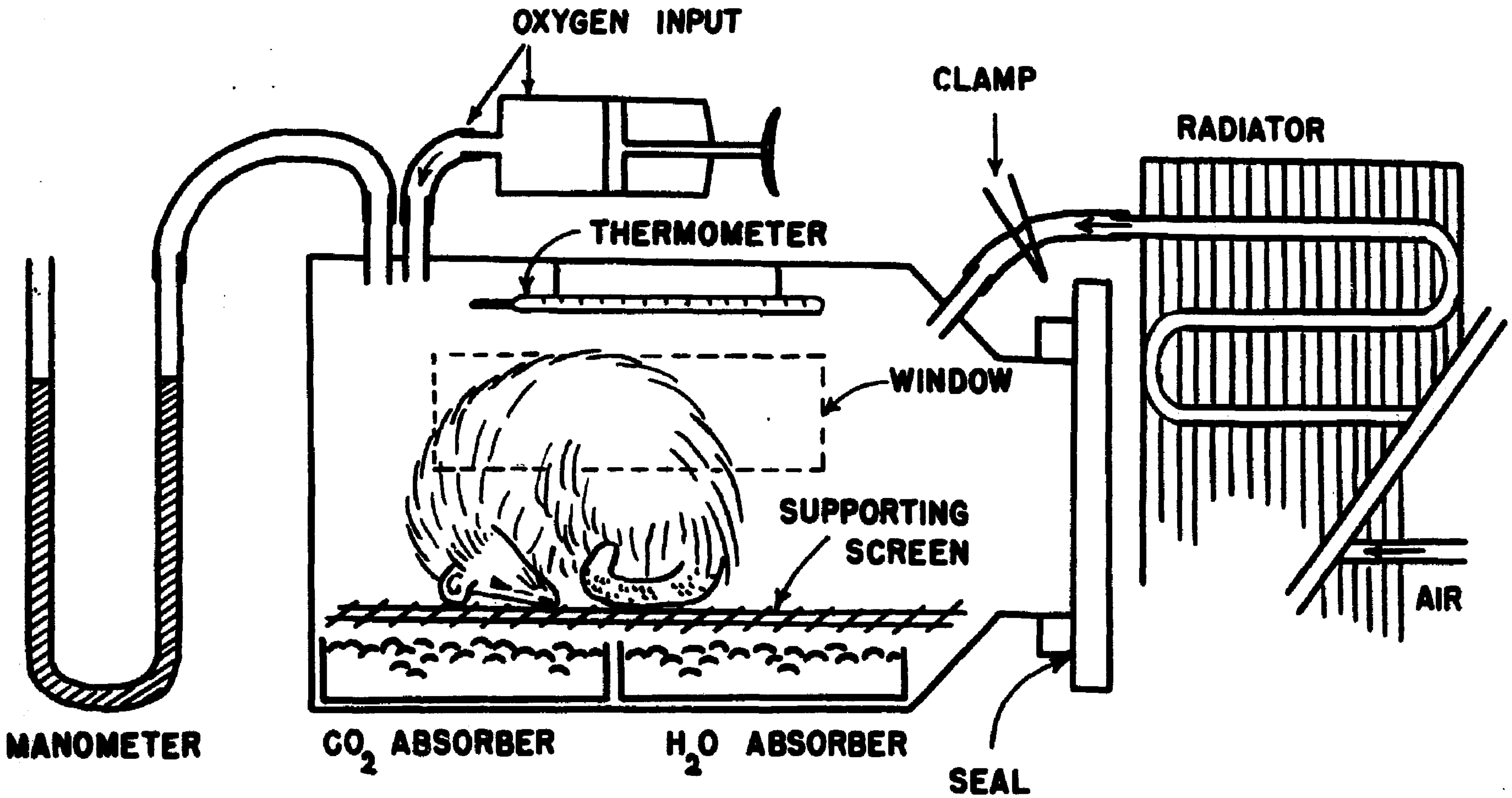
Five wild, mature opossums ranging in weight from 2.07 kg to 4.79 kg were used. These individuals were different from those in the food balance study. Each animal was held in a hardware cloth cage approximately 120 x 60 x 60 cm in size with doors at each end of the cage. One end of the cage, 60 cm in length, was closed off from the remaining portion of the cage providing a dark nest box. The small entrance to the nest box could easily be sealed and the door at the nest-end of the cage opened to facilitate capture or record body temperature. Cages were kept in an unheated garage in which the temperature ranged from -15° to 36°C. Bedding consisted of rags or excelsior. Dog food was provided every second night. Water was constantly available. During short periods of severe winter cold when animals slept almost continuously, no food or water was offered for the duration of the cold spell, usually less than one week. Animals were not fed for 40 hours prior to metabolism measurements to obtain the post-absorptive condition.

Calibrated mercury thermometers were used to measure ambient and body temperatures. A tube containing a thermometer projected into each nest box for ambient temperature (T_A) readings. A thermometer was inserted rectally to a depth of 10 cm to obtain body temperature (T_B) values. Body temperature readings did not increase with deeper insertion and are probably a good estimate of "core" temperature. All resting T_B determinations were made between 12:00 a.m. and 3:00 p.m., when animals were asleep. Although animals woke up while their temperatures were being taken, T_B values seemed representative for the sleeping condition since no T_B change was noted from sleep to arousal. As a general rule, opossums were handled gently and sparingly and showed little reaction to my presence.

Oxygen consumption was determined using a closed-circuit respirometer. A chamber (Figure 2) constructed from a standard milk can (40 l) proved to be particularly satisfactory, especially as to size. A plexiglass window in one side permitted observation of the opossum and a thermometer clamped within the chamber. The chamber had three tube outlets. One was connected to a manometer; oxygen was injected into the second outlet through a short rubber tube; the laboratory air supply, cooled through a radiator, led into the third outlet.

A primary object of this study was to obtain oxygen consumption values from acclimatized animals under prevailing environmental temperatures. Consequently, the animals were never brought into heated buildings and the metabolism measurements were made outdoors. Prior to metabolism measurements, each animal was weighed. Body temperature was taken at arousal and presumably was that of the animal asleep in the chamber. The chamber temperature was allowed to stabilize for one hour prior to oxygen consumption measurements. Generally, the chamber temperature was slightly higher than surrounding air temperature, although never more than 5°C higher. Fifty milliliters of oxygen were injected from a syringe for each measurement; the length of time required to consume the oxygen as determined by the manometer, was used to calculate oxygen consumption. Readings for oxygen consumption were rejected if chamber temperatures recorded at the beginning and end

Figure 2. Diagram of respirometer used in oxygen consumption determinations. Between determinations, the syringe was disconnected from the oxygen input port, providing an air outlet. During determinations the air supply was clamped off.


OXYGEN INPUT
CLAMP
RADIATOR
THERMOMETER
WINDOW
SUPPORTING SCREEN
AIR
MANOMETER
CO_2 ABSORBER
H_2O ABSORBER
SEAL

of each measurement period were not identical. Air was circulated through the chamber between oxygen consumption measurements. Mean barometric pressure recorded at the site was used to correct for STP conditions.

Carbon dioxide and water vapor were absorbed by sodium hydrate asbestos (Ascarite) and indicating anhydrous $CaSO_4$ (Drierite, residual H_2O in gas .005 mg/l) respectively. Generally, the total absorption surface of 400 cm^2 for each absorbant was found to be quite adequate. In other, similar investigations, small circulating fans have been used in closed circuit respirometers to maintain air in constant contact with absorbing chemicals. However, a fan was deemed undesirable here from the standpoint of duplicating the thermal environment in a ground den. Initial oxygen consumption data obtained without a fan followed expected patterns and it soon appeared that inhalations and exhalations of experimental opossums provided sufficient air circulation in the relatively small chamber space. Oxygen consumption values obtained here agree with energy determinations by food balance calorimetry. The abreviations "BMR" and "RMR" used here stand respectively for "Basal Metabolic Rate" as it is usually defined, and "Resting Metabolic Rate". The latter category applies to sleeping and quietly resting animals.

Collection of Road-killed Specimens

The opossum may well be the most frequently killed mammal on southern Michigan highways. Winter road-killed specimens collected before the end of March are a good source of study material. Road-killed opossums collected from January through March, 1968, provided the following information:

1. Winter weight, sex and age characteristics, and decline in body weight through the winter season.
2. Characteristics of the fat depot and decline in body fat.
3. Air temperatures at which animals were active.
4. An estimate of population distribution and range.
5. A qualitative analysis of stomach contents for a few specimens.

The Michigan Department of Natural Resources issued a statewide field order to its personnel to collect road-killed opossums. Each collected animal was sealed into a heavy duty polyethylene (turkey size) bag and pertinent information recorded on the attached tag. Specimens awaiting pick-up were placed in freezers or outdoors in barrels away from the sun. Generally, opossums processed as late as one month after collection were still in good condition for the purposes of this study.

All animals were sexed, and aged as juveniles or adults. Females were aged according to pouch discoloration

(Petrides, 1949). Many males and females could be aged by size alone. In a few cases, dentition (McCrady, 1939) was used. At the beginning of winter, one useful criterion is the condition of ears and tail. These appendages are blunted by freezing in animals that have lived through a previous Michigan winter.

Measurement of Body Fat

Theoretically, an animal body can be divided into fat and fat-free components. On this basis, if the densities of fat and fat-free components are known, the unknown amount of fat in an animal body can be calculated if the specific gravity of the carcass is determined by water immersion. By this technique, body fat has been estimated for men (Behnke et al. 1942, Fidanza et al. 1953), guinea pigs (Rathbun and Pace 1945, Morales et al. 1945), albino rats (Da Costa and Clayton 1950), cattle (Kraybill et al. 1951) and swine (Brown et al. 1951, Kraybill et al. 1953). More recently, the specific gravities of guinea pigs, swine and humans have also been calculated by helium displacement (Liuzzo et al. 1958, Gnaedinger et al. 1963, Hix et al. 1967).

Body fat was determined for 54 road-killed opossums. Hair was removed with animal clippers. The viscera were dissected out, leaving genital organs, kidneys and fat posterior to the kidneys along the back. By weighing each carcass to .1 gm in air and in water, specific gravity was calculated from the relationship:

$$\text{Specific Gravity} = \frac{\text{Weight in Air}}{\text{Weight in Air} - \text{Weight in Water}}$$

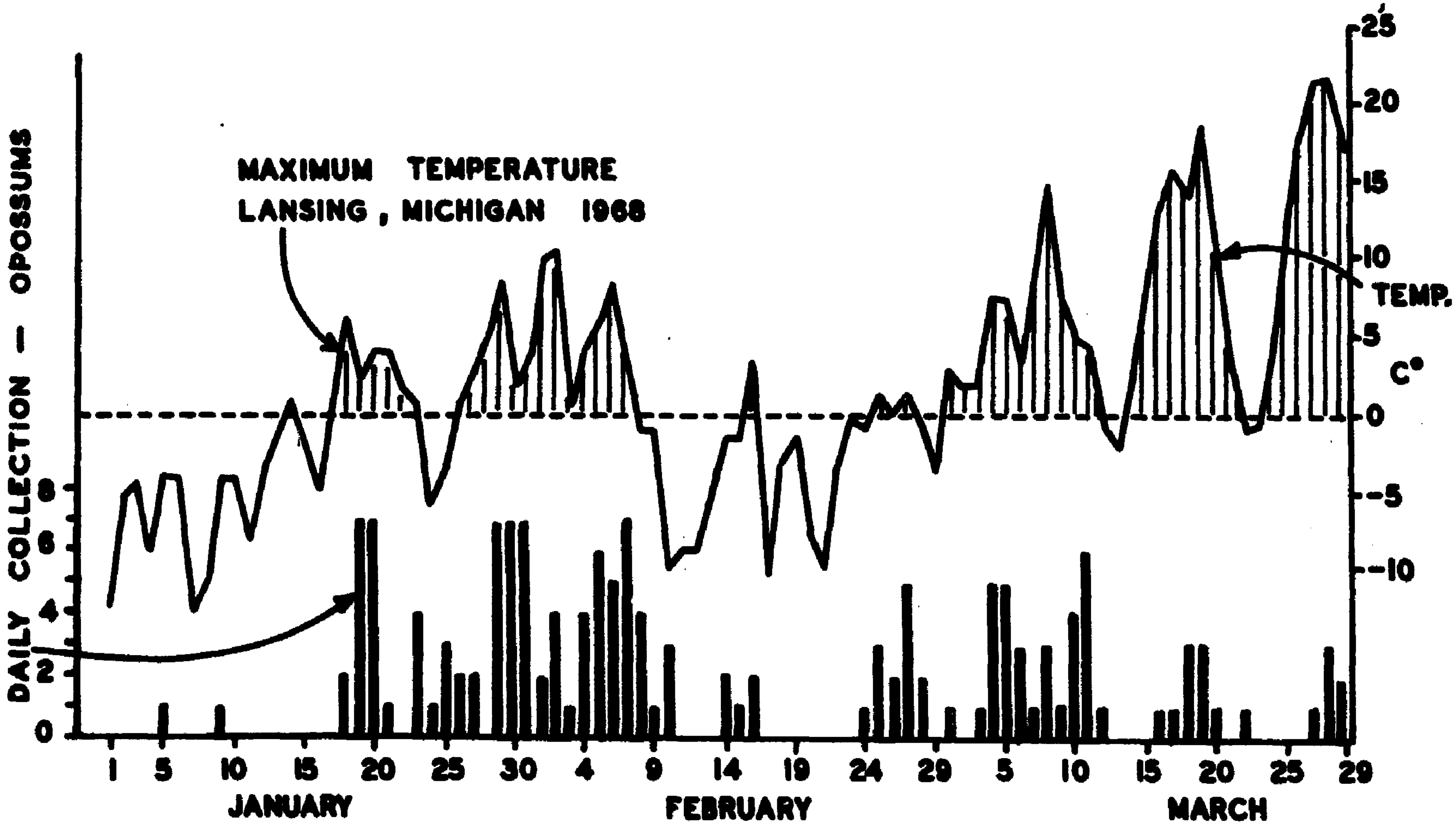
The eviscerated carcass was suspended from a triple beam balance pan by means of a small wire hook through the animal's nose. Detergent was added to the water to facilitate removal of air bubbles adhering to the carcass.

CHAPTER III

RESULTS AND DISCUSSION: ACTIVITY

The opossum tends to avoid freezing temperatures in winter and forages almost exclusively during periods of thaw. These generalizations are confirmed by my field observations, data from road-killed specimens and recorded activity of penned animals. In Figure 3, the daily collection of road-kills in southern Michigan from January through March is compared with the daily maximum temperature at Lansing for the same period. The daily maximum temperature, which usually occurs in the afternoon, has been chosen here for correlation with road-kill frequency because opossums are not entirely nocturnal in winter, but may venture forth in the late afternoon when temperatures are permitting. This is particularly true when the plane of nutrition is low, as will be shown in later chapters. Temperatures at Lansing were selected as being fairly representative for southern Michigan. It is evident that collection success was greatest when the maximum temperature exceeded the freezing level. Conversely, on days when the maximum temperature declined below freezing, collection success was minimal (Figure 3). These road-kill data, graphed according to five degree maximum temperature

Figure 3. The daily collection of road-killed opossums in southern Michigan compared to the maximum temperature at Lansing, Michigan, for the period January through March, 1968.


MAXIMUM TEMPERATURE
LANSING, MICHIGAN 1968
DAILY COLLECTION — OPOSSUMS
TEMP.
C°
25
20
15
10
5
0
−5
−10
8
6
4
2
0
1
5
10
15
20
25
30
4
9
14
19
24
29
5
10
15
20
25
29
JANUARY
FEBRUARY
MARCH

classes (Figure 4) shows a striking correlation between high collection success and above-freezing temperatures. Grouping all specimens collected (154 animals) according to two major temperature classes, i.e. above and below $0^{o}C$, the mean number of animals collected per day at temperatures below $0^{o}C$ was .56 (22 animals, 39 days); the mean was 2.64 per day for temperatures exceeding $0^{o}C$ (132 animals, 50 days). These means differ at the 1% level of significance ($t = 5.15$, d.f. = 87; (Snedecor 1956). It appears that the movement of opossums drops off markedly below $0^{o}C$, judging from these data and assuming that automobile traffic remains constant.

The activity of opossums shows similar relationships with temperature (Figure 5; Appendix A, Table 20). Activity was low or non-existant at sub-zero temperatures. It should be noted that each night as the temperature dropped, the activity of animals would usually span two temperature classes. However on some nights, total activity was included in one temperature class, or as many as four classes when the temperature declined as much as $15^{o}C$ during the night. For the whole period of 75 nights (559 opossum nights or 7.45 opossums per night), the mean activity span was 8.10 hours/animal/night, and the range of mean nightly activity spans was 2.2 to 13.7 hours/animal/night. The mean activity intensity was 5.07 activity units/animal/hour and the range of mean nightly activity intensity was 1.79 to 11.62 activity units/animal/hour.

Figure 4. The mean daily collection of road-killed opossums collected in southern Michigan from January through March, 1968, plotted according to 5°C maximum temperature classes at Lansing, Michigan. Lower limits of temperature classes are shown in the figure, the classes extending for 4.9°C, e.g. 0° to 4.9°, 5° to 5.9°C, etc.

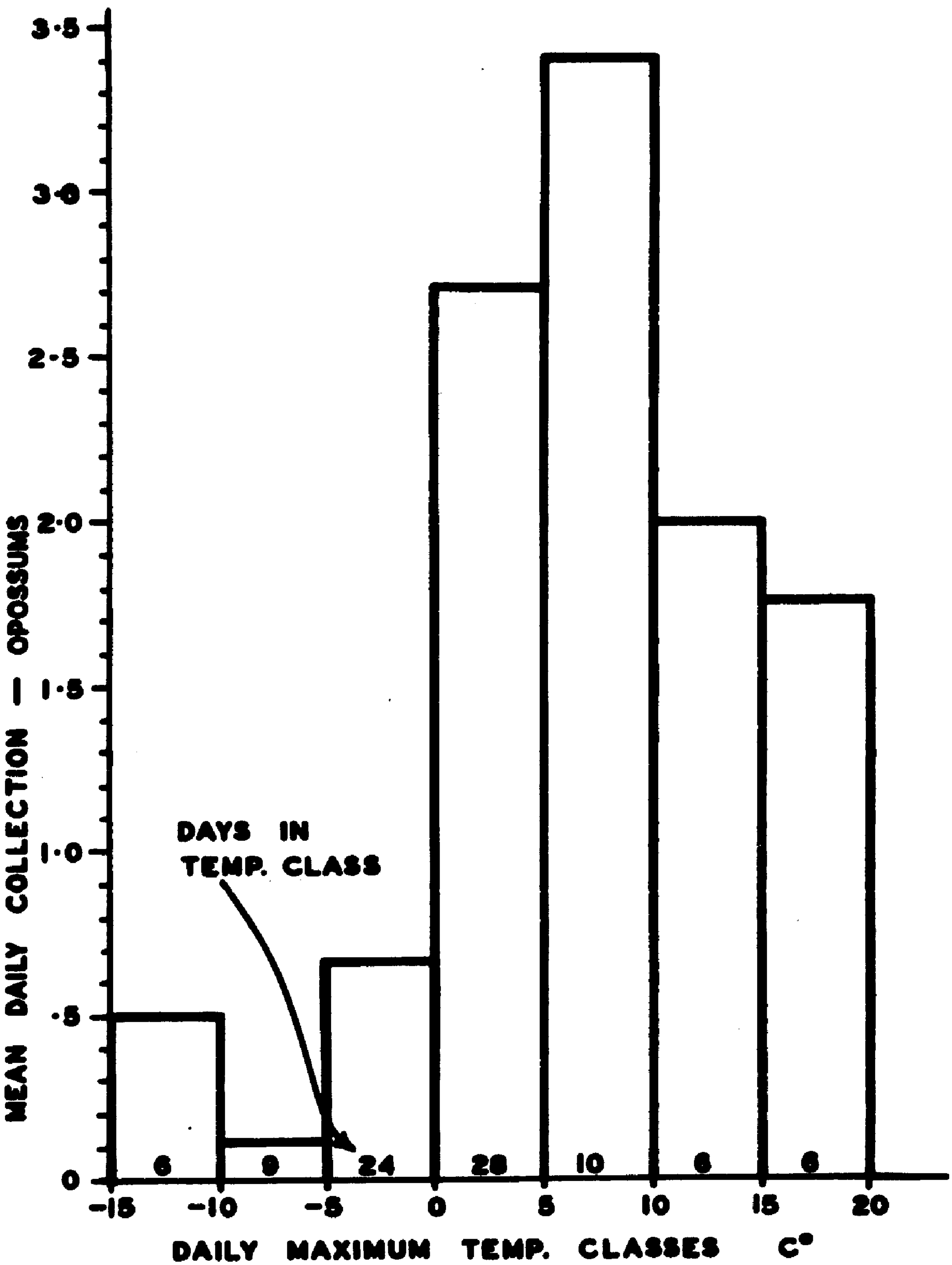
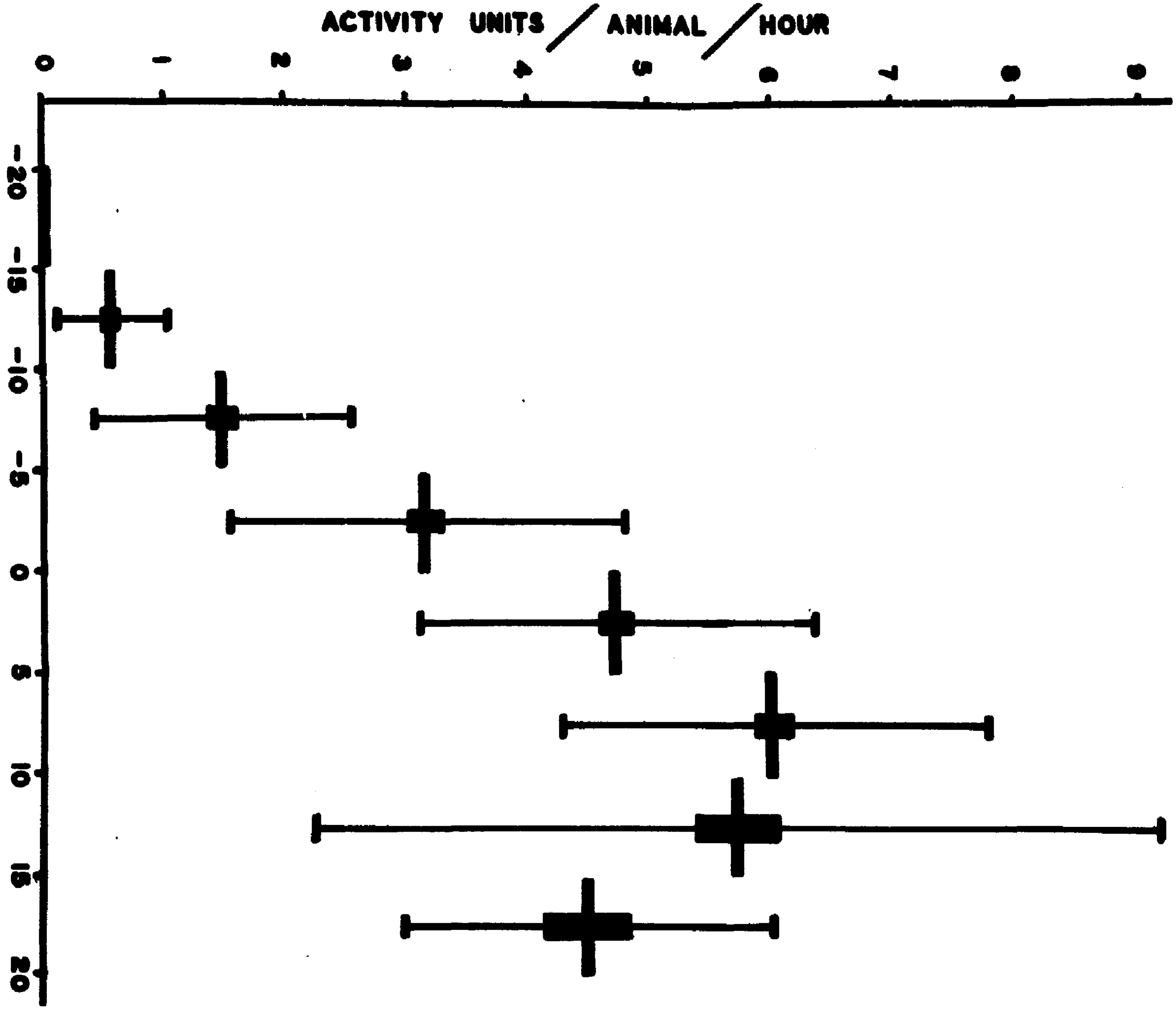

MEAN DAILY COLLECTION — OPOSSUMS
3·5
3·0
2·5
2·0
1·5
1·0
·5
0
DAYS IN
TEMP. CLASS
6
9
24
28
10
6
6
-15
-10
-5
0
5
10
15
20
DAILY MAXIMUM TEMP. CLASSES C°

Figure 5. Activity intensity (activity units/animal/hour) of opossums confined in experimental pens plotted according to 5°C temperature classes February 18 to May 3, 1968. Data are for 559 opossum nights, or 7.45 opossums per night for 75 nights. Temperatures were measured at the pen site. Lower limits of temperature classes are shown in the figure, the classes extending for 4.9°C e.g. 0° to 4.9°, 5° to 5.9°C, etc. Probing activity is explained in the text.



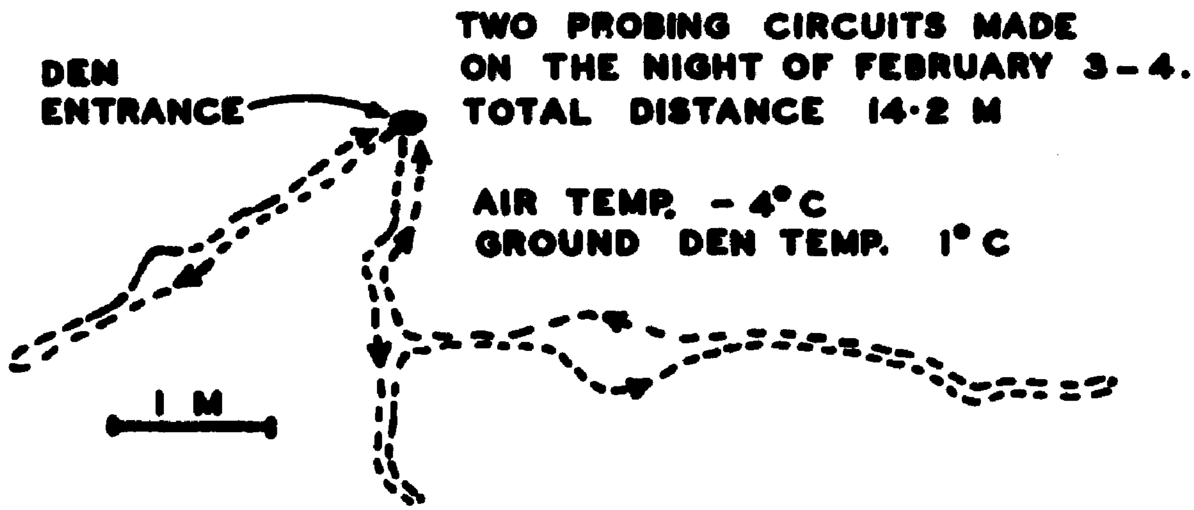
ACTIVITY UNITS / ANIMAL / HOUR
0
1
2
3
4
5
6
7
8
9
-20
-15
-10
-5
0
5
10
15
20

At sub-freezing temperatures, the opossum displays an activity pattern which I shall term "probing activity." Apparently, opossums monitor temperatures and other conditions of the macroenvironment by leaving the nest chamber and coming up to the ground den entrance. Probing activity may be extended into a small travel circuit in the vicinity of the den. Typically, a probing animal will stand at the den entrance, sniffing the air. The length of time at the den entrance varies. For example, on the night of February 20-21, 1968, the air temperature was -8°C at 6:00 p.m. and declined to -20.5°C by 1:00 a.m. Six of the eight experimental animals came to the entrance from one to 14 times between 6:00 p.m. and 1:00 a.m. The other two animals did not come to the den entrance and may have slept without interruption. The length of time each animal stood in the entranceway varied from 2 minutes to 15 minutes (21 observations) and the mean probing time was 5.8 minutes per animal. On the following night, the temperature was -10.5°C at 5:00 p.m. and -15°C at midnight. Probing activity was of shorter duration on this night, varying from 1 to 8 minutes in length, and averaging 3.2 minutes (21 observations six animals). Most probing activity on the night of February 21-22 began at 7:00 p.m. and ended around 10:00 p.m. In terms of activity units (units/animal/hour), I have observed that most activity up to about 2.5 units/animal/hour represents probing activity. In the field, short trails made in the snow at air temperatures below $0^{o}C$ are often a manifestation of probing activity. Such probing trails are quite distinctive, being limited track circuits that leave the den entrance but soon return (Figure 6). Sometimes probing circuits of several successive nights may be recognized at natural dens (Figure 6 and 7). In this connection, Wiseman and Hendrickson (1950) studying Iowa opossums, state, "...on two occasions, when night temperatures were $20^{o}F$ ($-6.7^{o}C$), tracks from ground dens made a circle of a few feet and returned." They also state that opossum activity is negligible below $20^{o}F$.

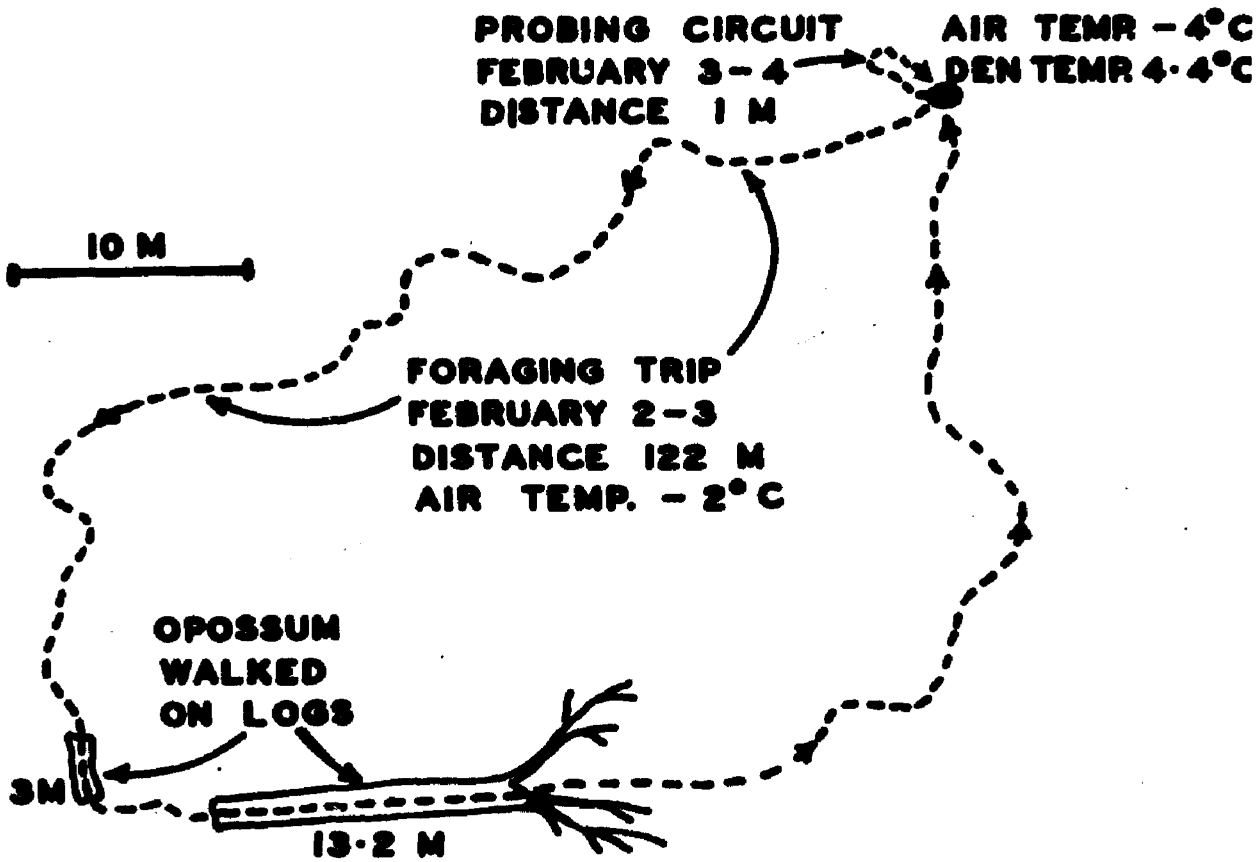
There is some individual variation in the inclination of opossums to expose themselves to freezing temperatures. One large penned male remained conspicuously above ground at temperatures as low as $-5^{o}C$, sleeping in the tree den in preference to the ground den. Apparently the ground den was quite suitable to other opossums rotated through this pen. It is perhaps significant that this experimental animal was the only one which ultimately died of starvation.

Contrary to much popular opinion and frequent statements in the literature, sub-freezing temperatures <u>per se</u> are apparently <u>not</u> detrimental to the health of opossums, <u>when they are well-fed.</u> In this study, caged animals held in an unheated garage for oxygen consumption and body temperature measurements remained in good health exposed to winter temperatures as low as $-15^{o}C$. However, these

Figure 6. Diagrams of probing circuits and a short foraging trip. The foraging trip appeared to be entirely unsuccessful.



TWO PROBING CIRCUITS MADE
ON THE NIGHT OF FEBRUARY 3-4.
TOTAL DISTANCE 14·2 M
DEN
ENTRANCE
AIR TEMP. -4°C
GROUND DEN TEMP. 1°C
1 M



PROBING CIRCUIT
FEBRUARY 3-4
DISTANCE 1 M
AIR TEMP. -4°C
DEN TEMP. 4·4°C
10 M
FORAGING TRIP
FEBRUARY 2-3
DISTANCE 122 M
AIR TEMP. -2°C
OPOSSUM
WALKED
ON LOGS
3M
13·2 M

Figure 7a. A probing circuit made in an aspen stand on the night of March 12-13, 1968. The ground was covered by 10 cm of new snow and the minimum temperature during the night was $-12^{\circ}C$. The total distance traveled by the opossum from its den located in the left background was 1.2 m.

Figure 7b. A probing circuit made by the same opossum on the following night of March 13-14. This circuit, at the left of the photograph, leads from the den located in the left background. The probing circuit at the right is the one from the previous night, pictured in Figure 7a. The snow-free area in the foreground was caused by melting of snow disturbed by the photographer. About 7 cm of snow remained on the ground from the previous day, and the minimum temperature during the night of March 13-14 was $-14^{\circ}C$.

animals showed signs of discomfort at temperatures below -10^{o}C as they shifted positions quite frequently. Their ears were frozen back to the head and their tails were shortened considerably by frost-bite. At winter's end these animals appeared in excellent condition, apart from their trunkated appendages.

The opossum appears to be more temperature sensitive than other predators of similar size associated with it. The striped skunk, raccoon and red fox occurred with the opossum on both study areas, and on occasion, occupied the same dens with it. Hence the relative temperature sensitivity of these species was quite apparent. At least some nocturnal activity was noted for the red fox for all winter nights for which data were recorded, regardless of temperature. Ables (1969) found that lower temperatures were associated with increased red fox activity in Wisconsin. Skunks and raccoons were not active on the coldest nights, particularly with deep snow on the ground. However, these species were frequently active at lower temperatures than the opossum. For example, on Area I, on the night of February 3-4, 1968 the air temperature at 9:00 p.m. was about -4^{o}C and snow covered the ground to an approximate depth of 4 cm. At two dens, opossums made probing circuits. However, skunks and raccoons made active forays that night. On the night of February 9-10, the air temperature was about -7^{o}C at 9:00 p.m. Skunks and raccoons were active, but opossums did not leave their dens. On the night of February 19-20, the air temperature was about -8°C at 9:00 p.m. Again, opossums did not leave their dens while skunks and raccoons were active. Sharp and Sharp (1956) report that the lower temperature limit for winter activity of Nebraska raccoons, discouraging 90% of the population, is 24°F (-4.5°C). In this study I found track evidence on several occasions of raccoon activity at air temperatures below -4.5°C when there was little snow cover on the ground.

The mean distribution of daily activity for 15 day periods from February 18 to May 3 is graphically illustrated in Figures 8a to 8e (Figures based on data in Table 21, Appendix A). It appears that the opossum is highly nocturnal when not restricted by low temperatures (Figures 8d and 8e). Generally, the first animals leave their dens around sunset; activity rises to a peak around midnight or slightly later, then declines and ceases around sunrise (Figures 8d and 8e). These data agree well with field observations. During the warm months of the year from late spring onward, wild opossums are to be seen at night with rare exceptions. During late winter and early spring the mean activity distribution appears to be strongly modified by low temperatures (Figure 8a). Mean activity commences at a low level at sunset but declines abruptly again around 8:00 p.m. as the mean nocturnal temperature dips below the minimum tolerance

Figure 8a. The mean daily activity distribution related to mean air temperature for 8 opossums for the 15 day period February 18 to March 4 (120 opossum nights). The mean times of sunrise and sunset are designated by symbols.

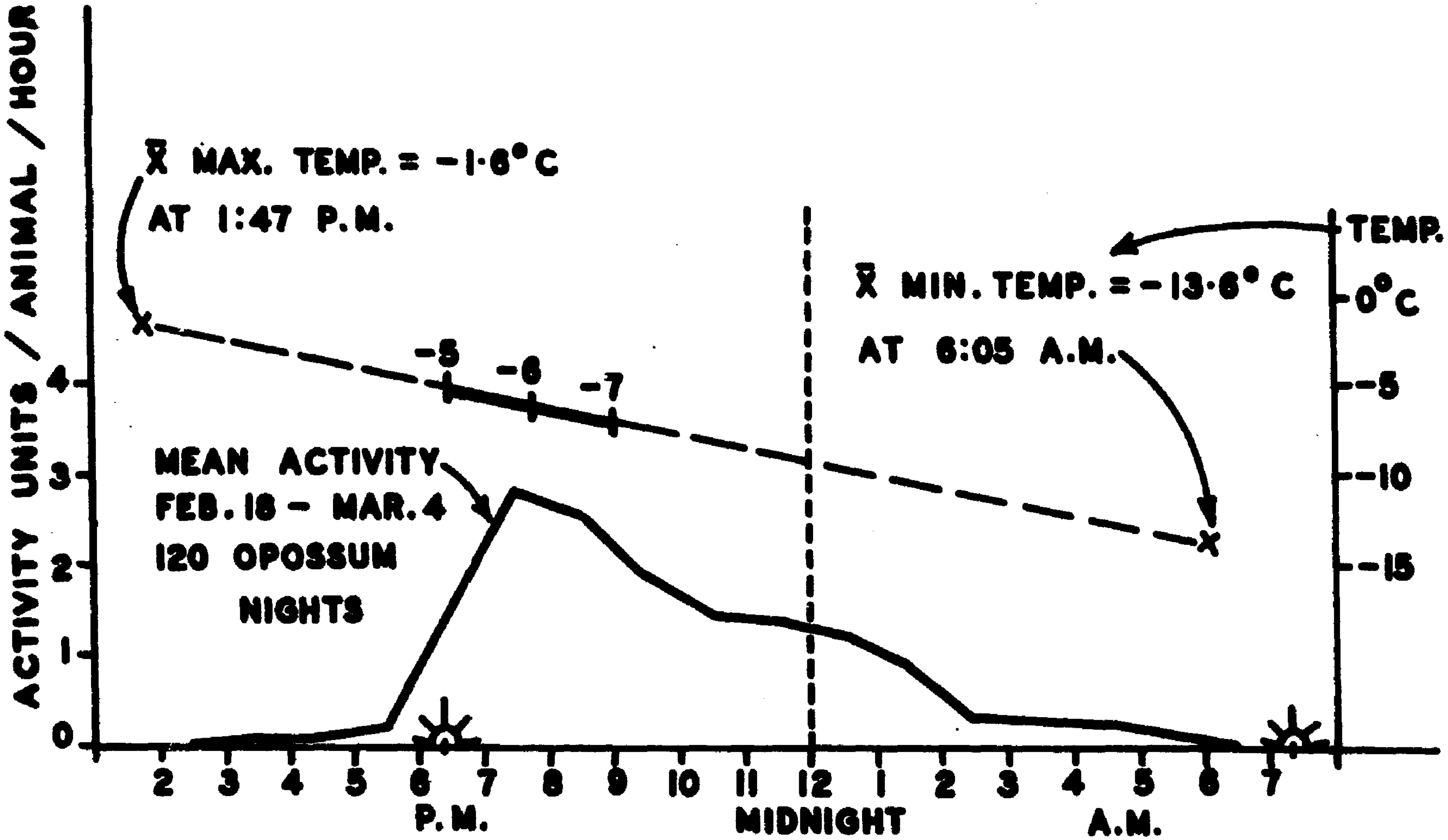

ACTIVITY UNITS / ANIMAL / HOUR
0
1
2
3
4
X̄ MAX. TEMP. = −1·6° C
AT 1:47 P.M.
−5
−6
−7
MEAN ACTIVITY
FEB. 18 – MAR. 4
120 OPOSSUM
NIGHTS
X̄ MIN. TEMP. = −13·6° C
AT 6:05 A.M.
TEMP.
0°C
−5
−10
−15
2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7
P.M.
MIDNIGHT
A.M.

Figure 8b. The mean daily activity distribution related to mean air temperature for 7 opossums for the 15 day period March 4 to March 19 (105 opossum nights). The mean times for sunrise and sunset are designated by symbols.

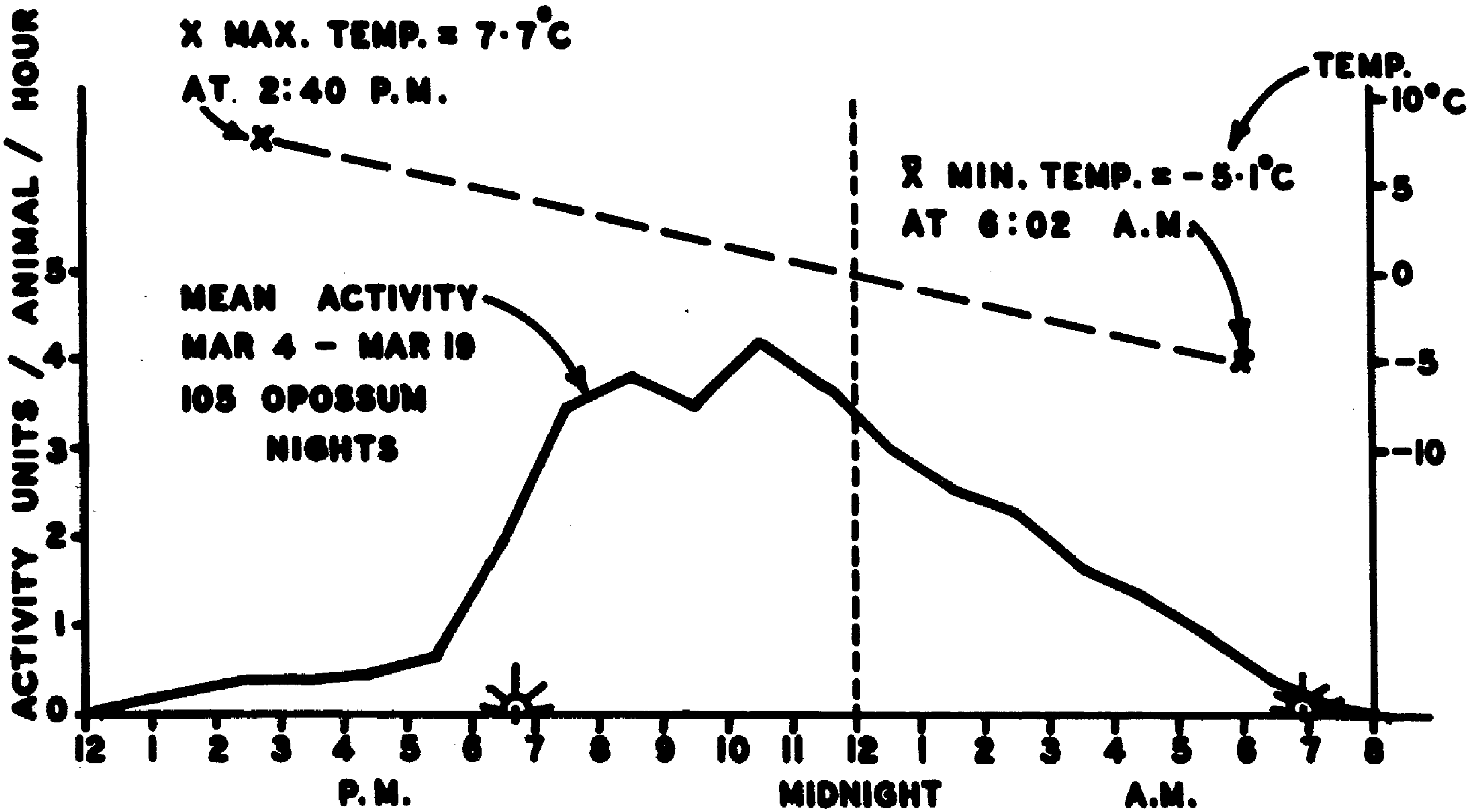
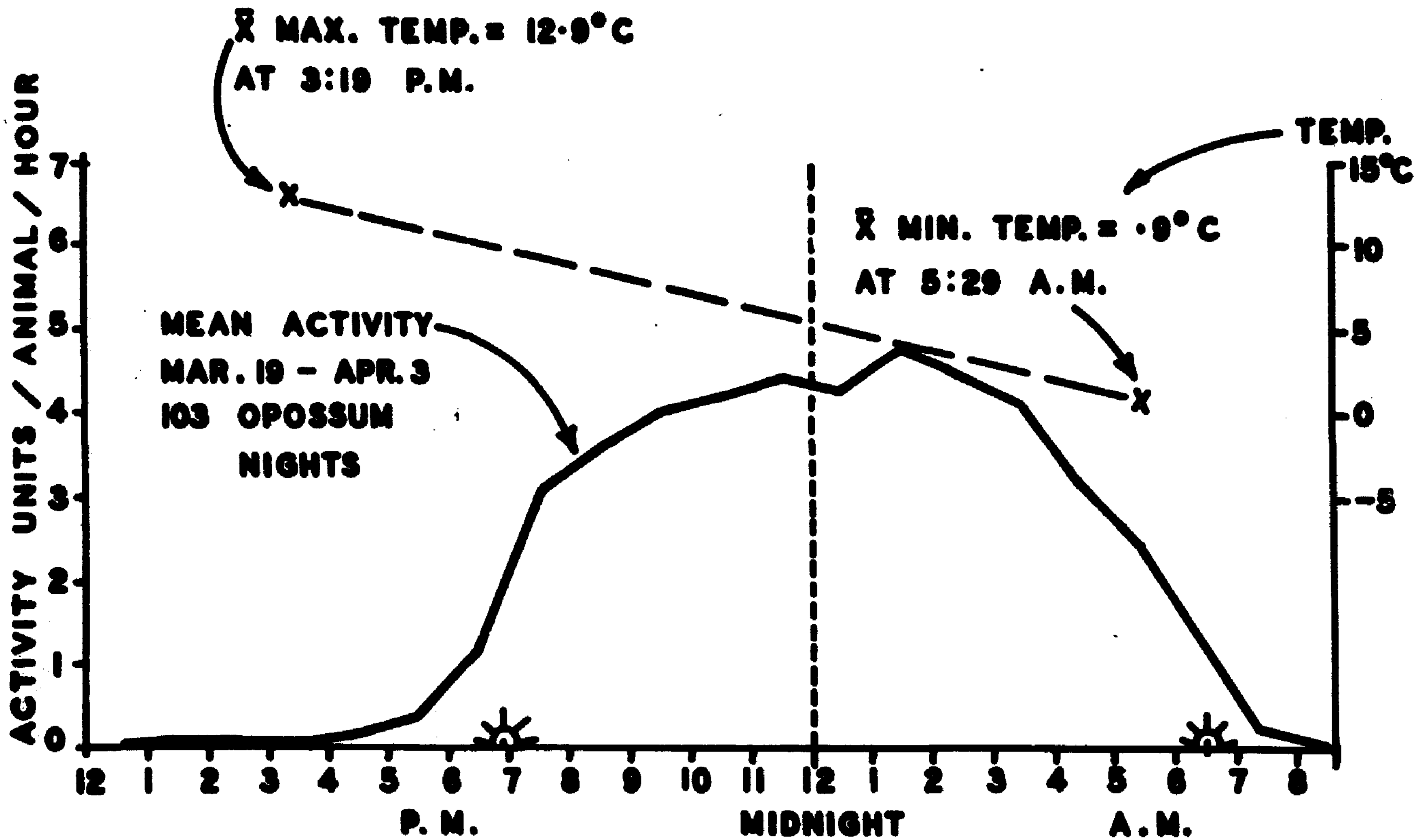

X MAX. TEMP. = 7·7°C
AT 2:40 P.M.
TEMP.
10°C
5
0
−5
−10
X̄ MIN. TEMP. = −5·1°C
AT 6:02 A.M.
MEAN ACTIVITY
MAR 4 – MAR 19
105 OPOSSUM
NIGHTS
ACTIVITY UNITS / ANIMAL / HOUR
0
1
2
3
4
5
12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8
P.M.
MIDNIGHT
A.M.

Figure 8c. The mean daily activity distribution related to mean air temperature for 6.9 opossums (daily mean) for the 15 day period March 19 to April 3 (103 opossum nights). The mean times for sunrise and sunset are designated by symbols.



$\bar{X}$ MAX. TEMP. = 12·9°C
AT 3:19 P.M.
$\bar{X}$ MIN. TEMP. = ·9°C
AT 5:29 A.M.
TEMP.
15°C
10
5
0
-5
MEAN ACTIVITY
MAR. 19 - APR. 3
103 OPOSSUM
NIGHTS
ACTIVITY UNITS / ANIMAL / HOUR
0
1
2
3
4
5
6
7
12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8
P. M.
MIDNIGHT
A. M.

Figure 8d. The mean daily activity distribution related to mean air temperature for 7.8 opossums (daily mean) for the 15 day period April 3 to April 18 (117 opossum nights). The mean times of sunrise and sunset are designated by symbols.

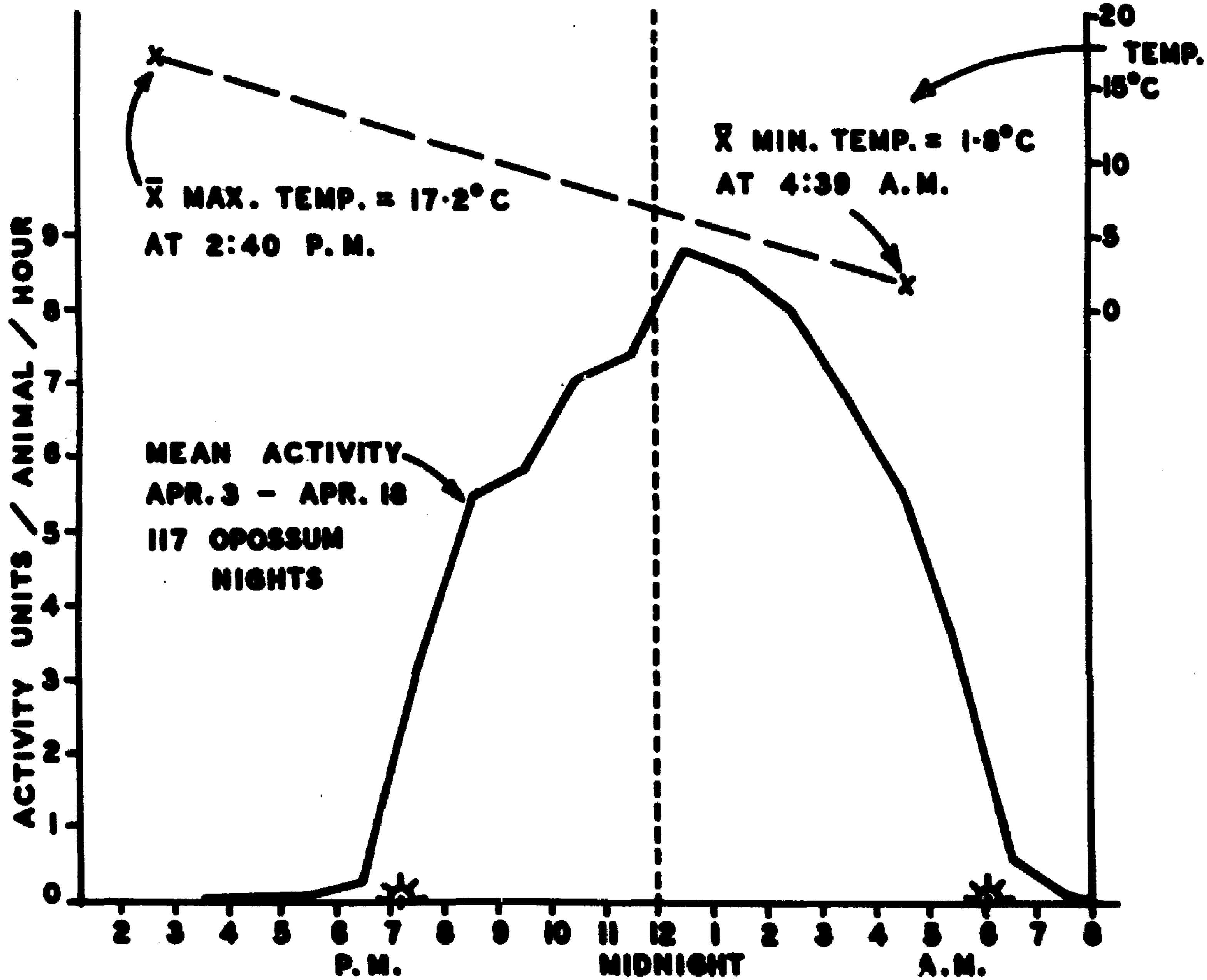
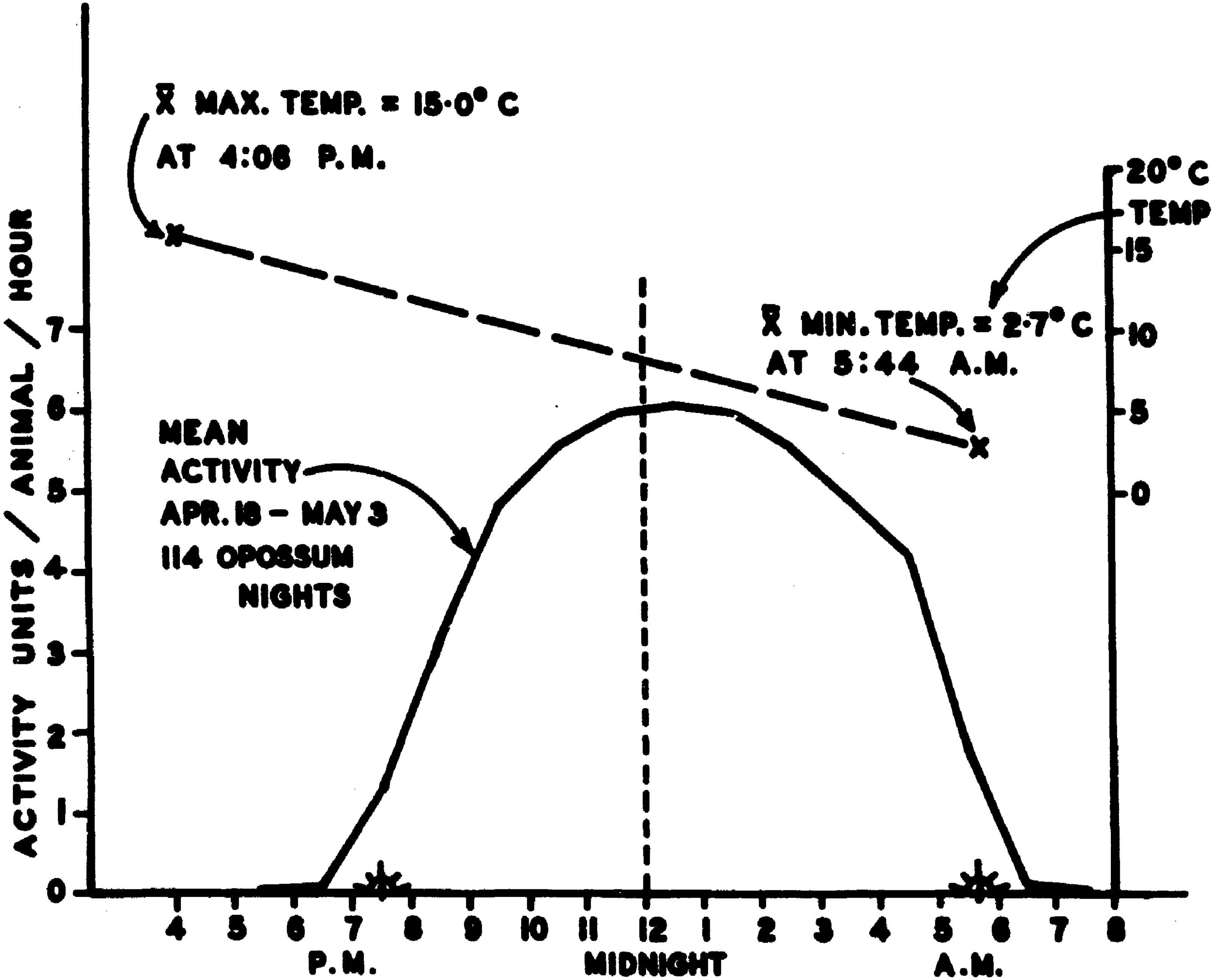

ACTIVITY UNITS / ANIMAL / HOUR
0
1
2
3
4
5
6
7
8
9
X̄ MAX. TEMP. = 17·2° C
AT 2:40 P.M.
MEAN ACTIVITY
APR. 3 - APR. 18
117 OPOSSUM
NIGHTS
X̄ MIN. TEMP. = 1·8°C
AT 4:39 A.M.
20
TEMP.
15°C
10
5
0
2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8
P.M.
MIDNIGHT
A.M.

Figure 8e. The mean daily activity distribution related to mean air temperature for 7.6 opossums (daily mean) for the 15 day period April 18 to May 3 (114 opossum nights). The mean times of sunrise and sunset are designated by symbols.


X̄ MAX. TEMP. = 15·0° C
AT 4:06 P.M.
X̄ MIN. TEMP. = 2·7° C
AT 5:44 A.M.
20° C
TEMP
15
10
5
0
MEAN
ACTIVITY
APR. 18 – MAY 3
114 OPOSSUM
NIGHTS
ACTIVITY UNITS / ANIMAL / HOUR
0
1
2
3
4
5
6
7
4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8
P.M.
MIDNIGHT
A.M.

level of about -5°C.

One of the major ecological problems encountered by this highly nocturnal species in the north is illustrated by the truncated activity distribution in Figure 8a. In late winter and early spring, most opossums are near the starvation point. During this period, often the only available foraging hours occur in the early afternoon when daily temperature maxima exceed the freezing level. Hence, in February and early March, opossums may be occasionally seen foraging in broad daylight, an extremely unusual circumstance at any other time in the year. Fitch and Sandidge (1953) describing the winter activity of Kansas opossums, write, "These occasional daytime forays seem to occur almost always in animals driven by hunger on winter days when the temperature has suddenly risen after periods of severely cold weather that have imposed activity and fasting."

I have observed a number of such foraging individuals in late winter, usually in an emaciated condition. One animal made periodic visits to an apple orchard to feed on rotten apples in March (Area I). Its route from den to orchard and back was identical in four visits. Its trips coincided so predictably with daily maximum temperatures that I anticipated its coming one warm afternoon and observed it feeding. To a lesser extent, the "temperature squeeze" on daily activity is also apparent in Figures 8b and 8c.

The high level of activity in early April (Figure 8d) is a reflection of increased sexual activity which reached a peak during this period. Although all animals were confined separately and without visual contact, males and females responded to each other. Animals would make clicking sounds by opening the mouth suddenly and slightly causing the lips to smack (see also McManus 1967). They would move around rapidly in the pens and occasionally utter a harsh cry.

Judging from field observations and activity data of penned animals (Figures 8a to 8e), two prominent features of the opossums daily activity pattern are as follows: (1) Activity occurs almost exclusively between sunset and sunrise except in late winter when it is apparently modified by a combination of extreme hunger and low environmental temperatures; and (2) nocturnal activity has a unimodal distribution with a peak near midnight. These activity characteristics appear to differ from those of other nocturnal species occurring with the opossum in one, or both respects. The raccoon is generally nocturnal in Michigan, yet tends to be somewhat active in daytime, especially in spring (Berner and Gysel 1967). Ables (1969) found crepuscular peaks of activity for Wisconsin red foxes, which appear to coincide with maximum prey activity. Ables reports that daytime fox activity is greater in winter than in summer. The cottontail rabbit is largely nocturnal, with an apparent annual cycle of activity between 5:00 p.m. and 7:00 a.m., according to roadside counts (Lord 1963). In spring and summer, rabbit sightings along roads reach a peak before sunset (Illinois, Lord 1963) and after sunrise (Lord 1963, and Kline 1965, Iowa). Apparently voles and mice also show bimodal activity peaks at dawn and dusk (Hatfield 1935, 1940, Hamilton 1943, Calhoun 1945, Brown 1956).

Winter snow appears to affect opossums primarily by covering the food supply and hindering travel. The opossum is poorly adapted to travel on soft snow, as it literally wallows through the snow with its low-slung body (Figure 9). Pruit (1960) classifies the opossum as a chionophobe (snow hating) after Formozov's (1946) classification system. Reluctance to emerge from the den after a heavy snowfall was illustrated by penned animals in mid-January, 1968. On the night of January 14-15, the air temperature remained at the freezing point most of the night. Two animals made probing circuits in their pens and two animals did not emerge from their dens but fed on snow at their den entrances. In the remaining four pens, den entrances were either completely blocked by snow or were marked by small openings in the snow.

In the field (Areas I and II), sub-freezing temperatures prevailed for the first half of January and the ground was covered by about 40 cm of snow. I found no evidence that opossums had emerged from their dens during this time. On January 17, air temperatures rose above

Figures 9a and b. An opossum weighing 1.83 kg, walking in fresh snow about 28 cm deep. Travel by this animal was extremely laborious; its tracks sunk in to a depth of 12 to 14 cm and its belly was dragging constantly. This opossum was placed in the snow for the photograph. At no time did I find indications that wild opossums venture forth in fresh, soft snow of this depth.

the freezing point marking the beginning of a six-day thaw. Tracks showed that some opossums had been active on the night of January 17-18, but apparently not in open areas where the snow was still soft. I followed two foraging trails in a pine plantation (Area I) where dripping melt-water from the foliage had frozen to a crust on the snow surface. These trails were entirely confined within the limits of the crusted area under the pines. These animals veered away whenever they encountered the soft snow at the periphery of the plantation.

A possible indication of discomfort in the snow is the opossum's frequent habit of walking on fallen trees and logs where these are available (Figure 6), rather than on snow covered ground. Perhaps discomfort is due to the rapid heat loss from the bare, uninsulated toes in contact with snow.

The opossum's locomotion appears to be greatly restricted by deep, soft snow. However, within the opossum's range in southern Michigan, restriction of locomotion per se by deep snow is probably a minor limiting factor. There are, I believe, two reasons for this: Firstly, mean snow depth is considerably less in southern Michigan than in many areas farther north, as will be discussed in Chapter XI. Usually, frequent thaws rapidly reduce deep snow cover following each snow storm in this region. Secondly, an ice crust forms rapidly on fresh snow during periods of thaw when opossums are active. Only a thin crust is necessary to support an average sized opossum of about 2.5 kg. This species has a fairly slow and even mode of locomotion and each foot places minimum stress on the substrate as the body weight is gradually shifted onto it.

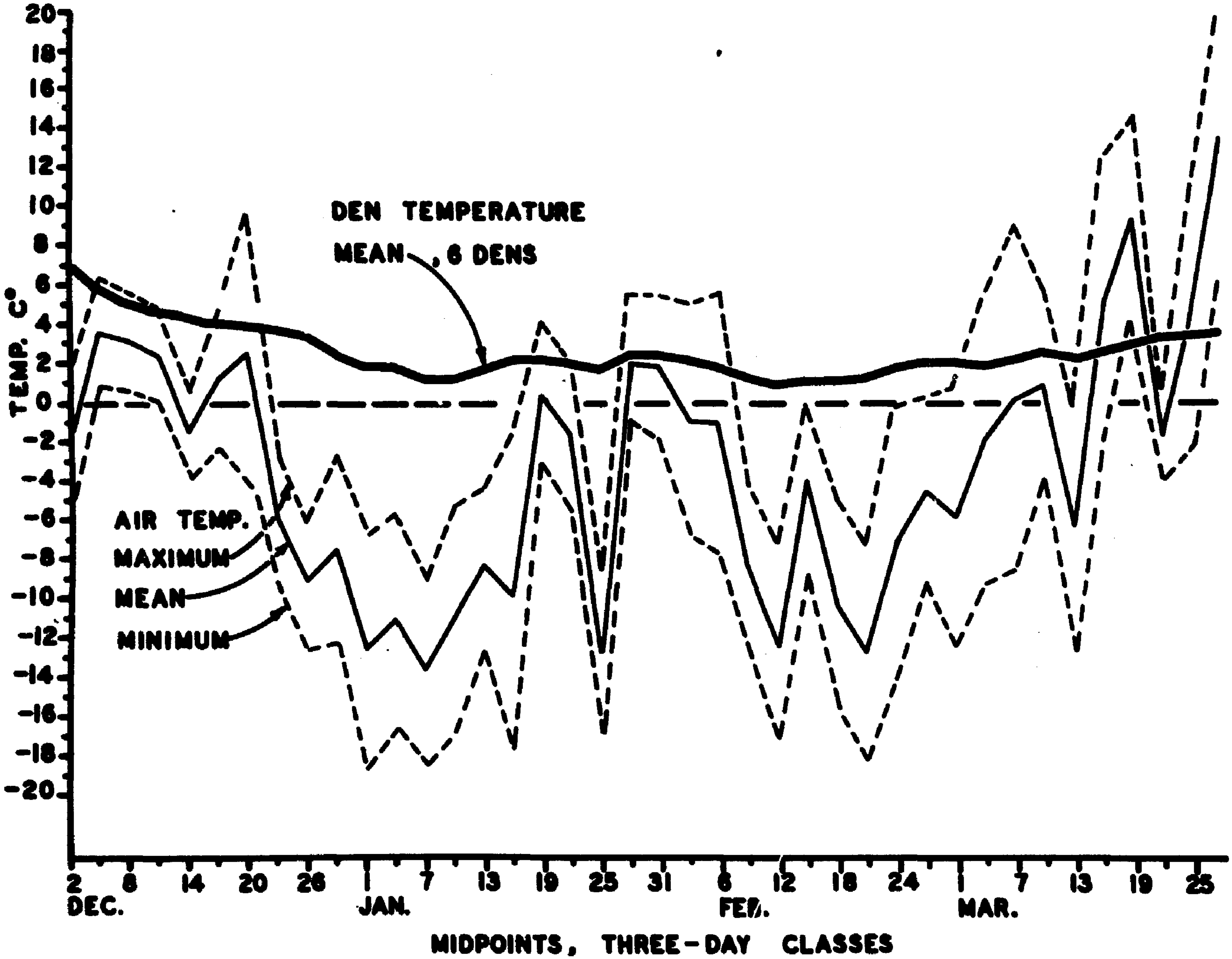
CHAPTER IV

DEN MICROCLIMATE AND ECOLOGY

In winter, opossums generally use ground dens according to my field observations in southern Michigan. Stuewer (1943) similarly found that opossums used ground dens exclusively in winter in south-western Michigan. Preference for ground dens over other den sites in the northern environment has been reported by Reynolds (1945) in Missouri, Fitch and Sandidge (1953) in Kansas, Wiseman and Hendrickson (1950) in Iowa, and Hamilton (1958) in New York.

Ground dens provide an extremely stable and ameliorated microclimate in winter. Winter temperatures of artificial ground dens in the pens compared to external air temperatures are given in Figure 10. Since ground den nest cavities were occupied by opossums most of the time, den temperatures are 1.0° to 1.5°C higher than they would have been if dens had been empty. A mean temperature increment of 1.51°C due to body heat was calculated from 109 comparative temperature measurements of dens with and without animals. Between December 1, 1967 and March 29, 1968, the highest recorded air temperature was 21.1°C while the highest recorded artificial

Figure 10. Three day temperature means for air and ground dens at East Lansing, Michigan for the winter of 1967-1968. Each plotted point for ground den temperatures represents the mean of 36 measurements, the maximum and minumum measurements daily for six dens over three day periods. The mean winter temperature fluctuation for ground dens was 0.3°C. On this graph, the daily temperature fluctuation would be represented by slightly more than the thickness of the den temperature line.


DEN TEMPERATURE
MEAN, 6 DENS
AIR TEMP.
MAXIMUM
MEAN
MINIMUM
TEMP. C°
20
18
16
14
12
10
8
6
4
2
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
2 DEC.
8
14
20
26
1 JAN.
7
13
19
25
31
6 FEB.
12
18
24
1 MAR.
7
13
19
25
MIDPOINTS, THREE-DAY CLASSES

den temperature was 6.4°C (n = 1440). The highest recorded daily mean for artificial dens was 6.3°C. The lowest recorded temperature for air was -22.8°C while the lowest recorded artificial den temperature was -1.1°C. The lowest daily mean for artificial dens was 0.6°C. The mean winter air temperature fluctuation for the 24 hour period was 9.9°C, and for ground den cativities it was 0.3°C. The winter temperatures of natural ground dens (n = 53) are given in Table I. A description of these dens is given in Table 19, Appendix A. In general, these values parallel those for artificial dens.

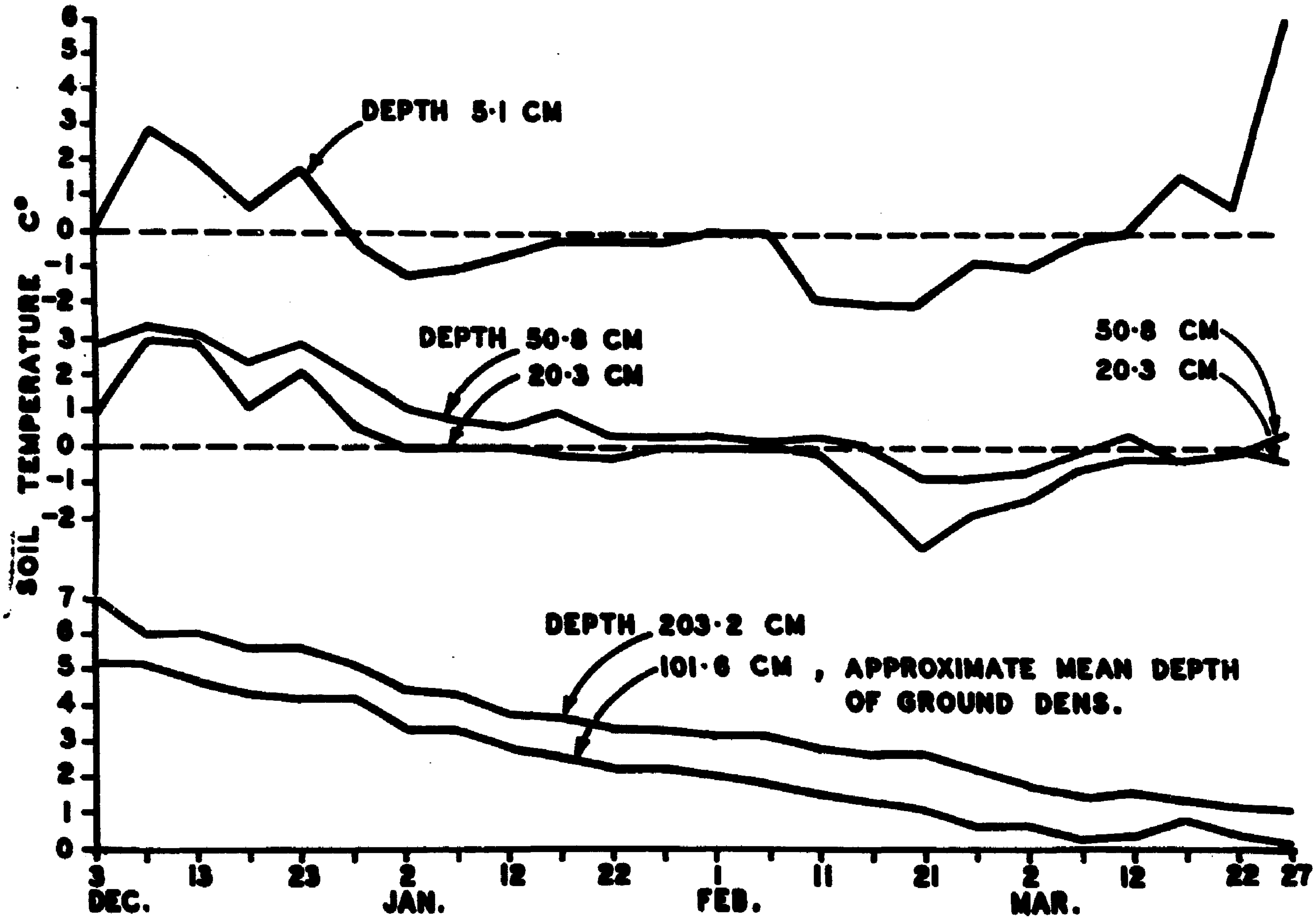
The dominant influence on ground den temperatures appears to be the heat budget of the soil. Soil temperatures for December through March at various depths are given in Figure 11. Soil temperature means are based on U. S. Weather Bureau data for East Lansing. It is apparent that the winter soil temperatures do not decline below the freezing point at the mean depth of ground den nest cavities (100 cm). However, soil temperatures appear to decline to their lowest level in March more slowly than ground den temperatures (Figure 10 and 11). Quite probably, this difference is due to the acceleration of convective heat loss by burrow air circulation.

Measurements presented here agree with those of most previous studies of den temperatures (Gerstell 1939, Linduska 1947, Hayward 1965, and Davis 1966) which have been of shorter duration and limited in scope. Winter

Table 1. Winter temperatures of natural ground dens at East Lansing, Michigan (Winter of 1967-1968). The range of air temperatures, 1 m above ground, was 21.1°C to -21.1°C for January through March, 1968.

Den No.	Number of Measurements	Mean Insertion Depth of Probe, CM	Mean Den Temperatures C° Jan.	Feb.	Mar.	Den Temp. Range (Jan-Mar) C°
1	10	213	-1.6	-1.6	2.2	-5.5 to 5.0
2	7	221	-	.9	3.6	-1.1 to 3.6
3	2	180	-	1.7	-	0 to 3.3
4	2	200	-	.3	-	- .6 to 1.1
5	8	158	-	1.3	1.7	0 to 3.3
6	13	212	3.4	2.3	3.6	-1.1 to 7.8
7	8	241	-	1.8	3.3	.6 to 4.4
8	3	200	-	1.4	-	1.1 to 1.7
Mean	(53 total)	203	.9	1.0	2.9	

Figure 11. Five-day soil temperature means for various depths of East Lansing, Michigan, for the winter of 1967-1968. The soil is level Miami fine sandy loam under fescue grass. The graph is based on United States Weather Bureau data, U. S. Dept. of Commerce.


DEPTH 5·1 CM
DEPTH 50·8 CM
20·3 CM
50·8 CM
20·3 CM
DEPTH 203·2 CM
101·6 CM , APPROXIMATE MEAN DEPTH OF GROUND DENS.
SOIL TEMPERATURE C°
3 DEC.
13
23
2 JAN.
12
22
1 FEB.
11
21
2 MAR.
12
22
27

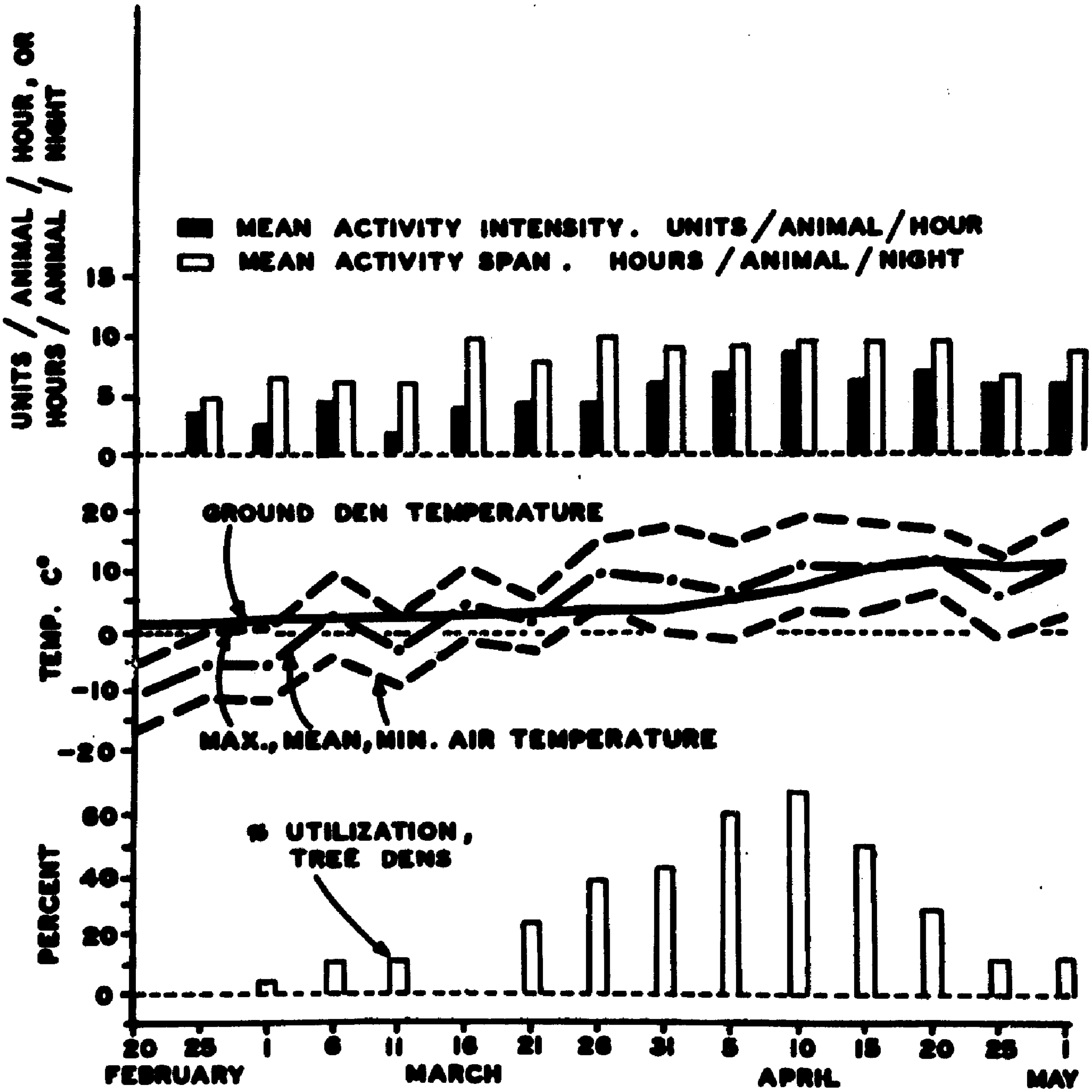
temperatures of one ground burrow as reported by Berner and Gysel (1967) are about 5°C to 7°C lower than values given here. The difference may be due to vertical insertion depths of the temperature probe less than those of the present study (Berner, personal communication). The great stability of the winter microclimate within ground dens is similar to that beneath the snow surface, although snow temperatures are somewhat lower (Formozov 1946, Pruitt 1958, Vose and Dunlap 1968). Stephenson (1969) measured winter temperatures in a Canadian beaver lodge. He found that they remained near the freezing point throughout the winter even though air temperatures declined to a mean minimum of -21°C.

The winter temperatures of other natural shelters such as tree cavities, hollow logs and brush piles tend to be lower and far less stable than ground den temperatures. A few temperature measurements of such shelters are as follows: On the morning of February 11, the air temperature was -9°C while an 8 m.p.h. wind was blowing. In the base of a large black oak tree (Area II), the cavity temperature was .5°C higher than the external air temperature. The thermometer probe was inserted upward into the tree trunk for a distance of 120 cm. On the same morning, temperatures were measured within a hollow elm log, 45 cm in diameter, and at ground level near the center of three large brush piles. In all cases, external and internal temperatures were found to be identical.

Other investigators report similar observations. Linduska (1947) found that temperatures at ground level near the center of brush piles in Area II averaged 1.4°C higher than external air temperatures for January, February and March. Gerstell (1939) in Pennsylvania reported that January temperatures within a hollow log were the same as those of the external environment; temperatures were about 2°C lower within a stump than outside. According to the data of Berner and Gysel (1967) for a raccoon tree cavity near the present study areas, the mean temperature within the tree cavity for January, February and March was -6.7°C, or 1.3°C cooler than the mean external temperature for the same period (these values are recalculated from their data). In mid-January, temperatures within this cavity declined to a minimum of -21°C (Berner 1965).

With the approach of spring and warm weather, opossums tend to use above-ground den sites more frequently than ground dens as the above-ground sites gain heat more rapidly. In the experimental pens, most opossums utilized tree dens or ground dens in spring in such a way that they appeared to gain a thermal advantage. In Figure 12, it is evident that the occupancy of artificial tree dens increased markedly as the mean air temperature rose above the temperature for ground dens, around March 16. By April 10, a majority of animals (six out of eight) were sleeping in tree dens during daylight hours (Figure 12).

Figure 12. The winter occupancy of tree dens and ground dens during daylight hours by eight experimentally penned opossums. Occupancy is compared to activity intensity, activity span, air temperature and ground den temperature for 1968. All plotted points and bars represent five-day means. Percent utilization of tree dens is complementary to that of ground dens. For example if 75% of the animals (6 animals) occupy three dens, 25% (2 animals) would occupy ground dens. Animals generally remained in their respective dens for the duration of the daylight period.


MEAN ACTIVITY INTENSITY. UNITS / ANIMAL / HOUR
MEAN ACTIVITY SPAN. HOURS / ANIMAL / NIGHT
UNITS / ANIMAL / HOUR, OR HOURS / ANIMAL / NIGHT
15
10
5
0
GROUND DEN TEMPERATURE
20
10
0
-10
-20
TEMP. C°
MAX., MEAN, MIN. AIR TEMPERATURE
% UTILIZATION, TREE DENS
60
40
20
0
PERCENT
20 25 1 6 11 16 21 26 31 5 10 15 20 25 1
FEBRUARY
MARCH
APRIL
MAY

Utilization of ground dens increased again toward the end of April when the mean air temperature declined below that of ground dens. During the summer months I have observed that opossums will use a variety of other den sites besides ground dens.

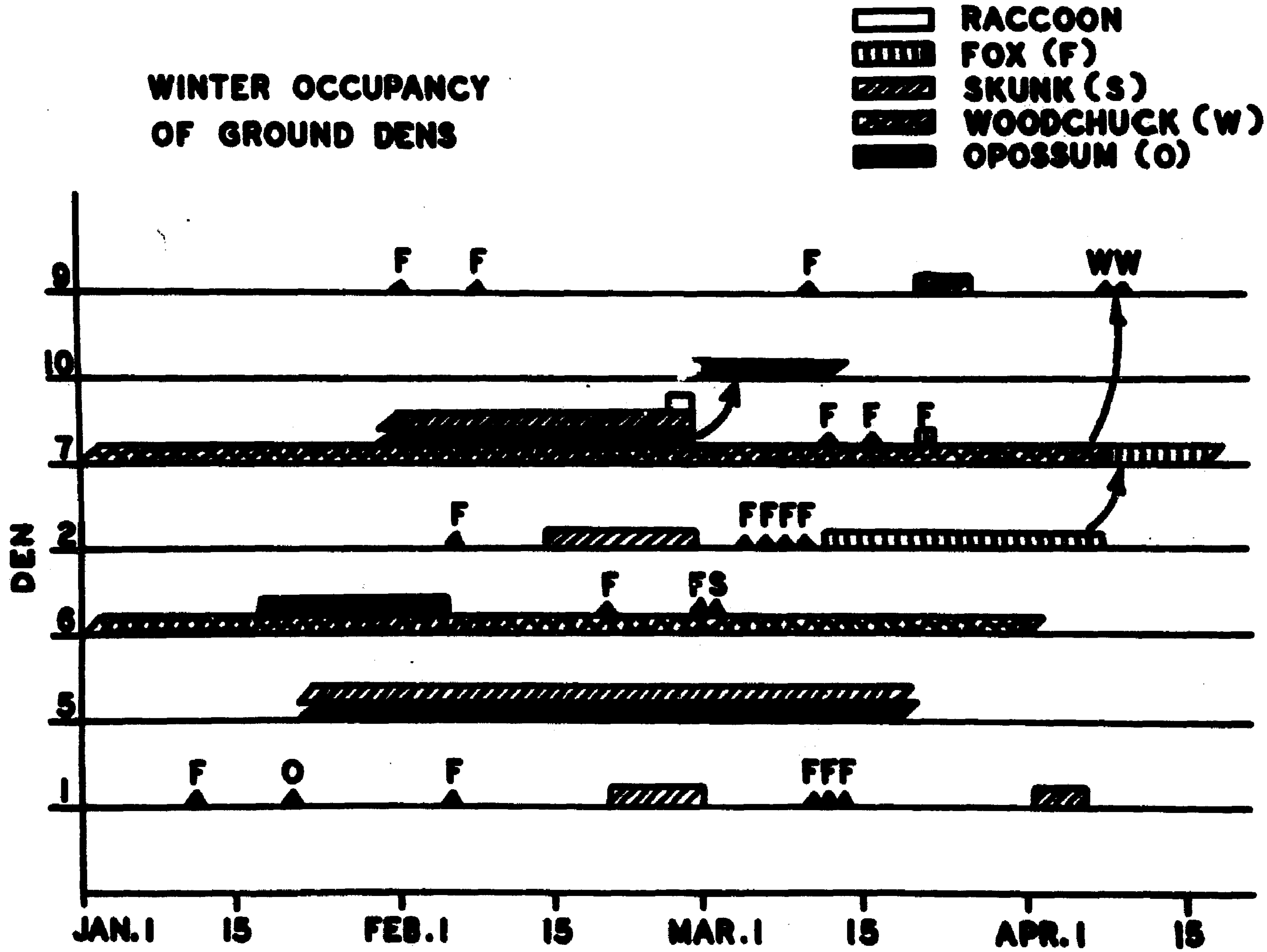
Opossums do occasionally occupy bulky leaf nests in winter in sheltered locations other than ground dens. I saw three such dens during the winter of 1967-1968, two in garages and one in a tree cavity. Temperature measurements within one of these nests in a tree cavity are of particular interest because they appear to confirm that a primary requirement for the winter den environment are temperatures which do not significantly decline below the freezing level, rather than a specific requirement for a particular den location. Opossums used nine ground dens in Areas I and II; however one animal in Area II occupied a cavity within a large spreading base of a black oak (Figure 41, Appendix B) for a period between January 21 and February 29. This large cavity was closely packed with oak leaves. On February 11, when the external air temperature was -7°C, the cavity temperature (within the nest) at a probe insertion depth of 190 cm was -.9°C; the opossum was in the den. Judging from two other temperature measurements of the same den in late February while the opossum was in the den, the temperature remained close to the freezing point in this tree cavity for the duration of winter. The microclimate within this heavily insulated tree cavity is very comparable to that of ground dens and very unlike that of most other tree cavities.

The two other leaf nests were in garages, one of which I investigated. This nest was a bulky affair, jammed behind implements and partly built into the rear wall of an unused garage. Two female opossums occupied the nest, sleeping about 30 cm apart. The nest was dismantled and contained about four bushels of maple and elm leaves. The garage owner said that he had seen the animals first in August, and that he had found a trail of leaves leading to the nest through the garage soon afterward. It is quite likely that opossums built these nests in the very interesting manner of carrying leaves in the coils of their tails (Lincecum 1872, Pray 1921, Smith 1941, and Nestell's letter in the appendix, 1969). Although I have not observed this behavior pattern directly, I found a trail of grass and debris leading into three ground dens within the experimental pens. The opossum's occasional winter use and more extensive summer use of den sites other than ground dens in Michigan suggests that its winter occupancy of ground dens is a matter of thermal advantage (selection is probably guided by comfort) rather than innate preference. Some evidence that denning behavior may vary with latitude is provided by Yeager (1939) who found that only 20% of winter dens in Mississippi were ground dens while 47% of the dens were in trees and logs.

Contrary to occasional statements in the literature, the opossum does not dig its own ground dens. It is obliged to use the ground dens excavated by other mammals, apparently because its grasping type of feet are unsuited for effective digging. Animals within experimental pens managed to escape by digging on only two occasions, even though the bases of the masonite pen walls were covered with dirt to a depth of merely 10 cm. One animal attempted to escape from a holding cage placed on the ground. It broke through the wire mesh floor of the cage but did not manage to dig under the cage. Another animal escaped from its cage in the garage. Its attempts to dig through the soft dirt under the garage door were quite ineffective although the opportunity to dig extended over the entire night period. At best, the opossums digging attempts result in shallow scrapes.

Generally, only a single opossum occupies a ground den at one time. However, individual opossums may spend the winter in the same den complex in company with other mammal species. The winter occupancy of seven ground dens in Area I, determined primarily by observation of tracks, is diagrammed in Figure 13 (temperatures for most of these dens are given in Table I; descriptions are given in the appendix). Den No. 5 with a single entrance held an opossum and a striped skunk continuously for at least two months. Den No. 7 (Figure 42, Appendix B) showed most signs of use by different species. During the course of the

Figure 13. The winter occupancy of seven natural ground dens in Area I by opossums and other mammal species. Each bar represents occupancy by a single animal; parallel, contiguous bars indicate simultaneous tenancy of the same den. Bars with square ends represent complete occupancy periods as shown. A slanted end to a bar indicates uncertainty as to the exact beginning or end of the occupancy period. Triangles represent burrow investigation or cursory use.


WINTER OCCUPANCY OF GROUND DENS
RACCOON
FOX (F)
SKUNK (S)
WOODCHUCK (W)
OPOSSUM (O)
DEN
9
10
7
2
6
5
1
F
O
FFF
FFFF
FS
WW
JAN.1
15
FEB.1
15
MAR.1
15
APR.1
15

winter it was occupied by five mammal species. There were four entrances to this den, only one of which was consistently used. On February 28, an opossum, striped skunk, raccoon and woodchuck occupied this den simultaneously, presumably in different chambers of the den complex. On February 29, the woodchuck emerged from hibernation and as I approached the den obscured from its vision, it uttered a series of gutteral barks. It continued barking in a bellicose manner until it saw me. Subsequently, the woodchuck was the sole tenant of this den complex, the opossum moving to a very inferior, untenanted den (Den No. 10) about 150 m away (Figures 7 and 13) where it remained until the middle of March. The woodchuck remained in Den No. 7 until early April when a family of red foxes raised in Den No. 2, took over Den No. 7. It is of interest that a red fox stayed overnight on March 23-24 in Den No. 7 (Figure 13) simultaneously with the woodchuck during a heavy snowstorm which left 27 cm of snow on the ground. In the Literature, Lay (1942) reported simultaneous den occupancy by an opossum and an armadillo in Texas. Sandidge (1953) in Kansas found evidence of one den housing both an opossum and a woodchuck. However, Reynolds (1945) in Missouri wrote, "At no time were opossums found occupying dens with other species of mammals."

These observations on the winter den tenancy of the opossum are not extensive. However, they do suggest that the opossum's winter den ecology neatly dovetails with that of other mammal species. During the winter, when energy conservation through the prevention of heat loss is vital to the opossum's survival, it occupies ground den complexes quite harmoniously with other species. In spring, the opossum's thermal dependency on the ground den ceases coincidentally with increased breeding competition for desirable dens by other mammals. However, the opossum's marsupium obviates the necessity of entering into breeding competition for dens. Hence, that portion of the opossum's ecological niche concerned with den use appears to overlap to a minimal degree with niches of other mammals. a circumstance predicated on the opossum's adaptable denning behavior.

CHAPTER V

FOOD AND FORAGING BEHAVIOR

The opossum appears to be a carnivore by preference and omnivore by necessity. The rapacity with which captive animals will attack living prey brought near them leaves little doubt about the opossum's dietary predilectious. Judging from the contents of twenty stomachs collected during January, February and March (Table 2) the winter diet of opossums consists largely of animals. Animal remains, primarily mammalian, occurred in 85% of the stomachs and plant remains were found in 35% of the specimens. Most plant material was fibrous debris and grass, apparently swallowed incidentally.

The importance of animal food in the winter diet has been noted by other workers. Taube (1942) examined 52 stomachs of Michigan opossums collected in September, November and December. He found that 81% of the total volume consisted of animal material, and 16.5% was vegetable. Eight specimens collected in March, April and May (Taube 1942) showed animals comprised 91% of the volume, and vegetable matter 9%. Dearborn's (1932) Michigan specimens showed an incidence of 70% animal material and 30% plant material. In New York (Hamilton 1958), the mean frequency of occurrence (n = 65) of various food items for the months of December through March are as follows, (means calculated from Hamilton's data): Mammals 60%, amphibians 20.2%, earth worms 32.5%, insects 22.9%, fruits 19.7% and green vegetation 48.5%.

Apparently, certain plant foods are utilized when they are available. It has been previously noted that one opossum was observed to make frequent forays to an apple orchard in March, where it would feed on rotten apples. The one specimen (Table 2) containing corn was killed adjacent to a large corn field close to Area I. Wiseman and Hendrickson (1950) reported that the bulk of the opossum's winter food in Iowa was corn, with insects next in importance.

The high incidence of mammals (70% occurrence, Table 2) in the winter diet is remarkable in view of the fact that the opossum can be outrun by almost all Michigan mammals. Apparently the opossum overcomes its disadvantage of low speed by surprising its victims at close quarters, or by eating carrion. Within lunging distance of its jaws, about 20 to 40 cm, the opossum visually recognizes mammalian food and acts swiftly. Yet, at a distance of about 1 m, it has difficulty recognizing a live mouse, judging from the behavior of captive specimens. I believe the ground burrow is of prime importance in providing a concentration point and occasional trap for the opossum's victims. Rabbits and mice are undoubtedly captured in the close confines of

Table 2. Stomach analysis of 20 opossums collected between January 23 and March 20, 1968.

	Frequency of Occurrence
Striped Skunk	1
Muskrat	1
Cottontail Rabbit	1
Whitetail Deer	2
Opossum	1
Shrew	1
Field Mouse	2
Unidentified Mammals	7
Garter Snake	1
Leopard Frog	1
Insects	3
Earthworms	2
Plant Fibers	7

burrows where their escape routes are cut off. Probably many, if not most, earthworms, insects, snakes and amphibians (Table 2) in the winter diet, are obtained below the frost line in ground burrows.

Apparently some mammal food is carrion. Two animals (Table 2) fed on whitetail deer carcasses. The muskrat remains in one stomach consisted of skin and fur, with no flesh or bone, indicating carrion origin. I doubt that the striped skunk remains in one specimen are the result of predation. Opossums probably locate some carrion in ground dens. Allen and Shapton (1942) reported finding dead striped skunks in three ground dens and a rabbit in another of the 36 dens they excavated and examined.

Opossums will readily eat their own kind. I have observed young opossums, three months old, feeding on a dead litter mate. Only one clear case of cannibalism was noted in the 20 specimens examined, although some opossum hair occurred in almost all stomachs. A case of cannibalism was observed in the experimental food balance study. A female opossum (2.08 kg) was introduced into a pen containing a dead opossum in the den cavity. This animal fed on the dead opossum from February 19 to March 16, apparently sleeping next to the carcass. The carcass began smelling on March 5. During this period, the total calculated energy cost of survival for the 2.08 kg opossum was 4167 kcal (metabolic rate based on food balance data). Of this amount, 1212 kcal were provided by dog food, leaving 2955 kcal to be provided by cannibalism. Using the combustion value of 1.37 kcal/gm wet weight for whole field mice (Golley 1960), the dead 2.0 kg opossum must have provided 2740 kcal of energy. These calculations indicate that the carcass was probably entirely consumed. From a nutritional standpoint, the unusually good health of this individual seemed to confirm that cannibalism provides the best ratio of amino acids in the diet.

Cannibalism may be a significant factor in the winter survival of opossum populations. Many opossums are born late in the year. Most of these specimens are rat-sized (less than 2 kg) at the beginning of winter and have a small chance of survival. Most opossums of this size collected in January, February or March, were at the starvation point, with exhausted fat depots (see Chapter IX). Such animals are quite likely to die in ground dens where they provide a potential energy source for other opossums. It is conceivable that the protein pool created by these late-born individuals contributes to the winter survival of some breeding stock.

An interesting sidelight of opossum nutrition in winter is the practice of coprophagy by this species. While following opossum trails in winter snow, I have observed evidence of coprophagy several times. Three of the experimental animals were observed to coprophagize. Refection by one of these opossums (No. 4, Figure 30, Appendix B) was quite regular in the first seven days in the metabolism cage.

Initially, a segment of the wire mesh cage bottom was covered by a small sleeping platform. Feces collecting on this platform were eaten by this individual. Subsequently, the platform was removed, preventing coprophagy. There was no change in the weight level maintained by this individual after coprophagizing had ceased, indicating that the energy derived from feces must have been minimal.

A number of workers have reported on significant nutritional benefits derived from coprophagy by rabbits and rats. Recycling of the gut contents harnesses bacterial activity in the lower intestinal tract and apparently has positive effects on the availability of the following nutrients: Vitamin K (Nightingale et al. 1947, Johanssen and Sarles 1949, Barnes and Fiala 1959, Mameesh and Johnson 1960, and Wostmann et al. 1963); Riboflavin and Niacin (Kulwich et al. 1953); Pantothenic acid (Fridericia et al. 1927, Kulwich et al. 1953 and Daft et al. 1963); and Vitamin B_{12} (Kulwich et al. 1953, and Barnes et al. 1957). What specific role coprophagy plays in the opossum's winter nutrition is an open question. It may be that refection supplements certain nutrients which decline to a critical level as much of the energy for winter survival is derived from body tissue catabolism.

The varied winter diet of the opossum reflects its opportunistic foraging habits. Winter trails appear to to wander aimlessly through the countryside. Yet, there seems to be a pattern. For example, on January 21, I followed the trail of one individual continuously for 2.55 km in 15 cm of snow. The maximum radial distance of this trail from the den of exit and reentry was 0.4 km. The trail led through several ecological types; percentages of the total length of the foraging trip are as follows: 65% lowland hardwoods including elm, ash and swamp white oak, 10% lowland swale with marsh grasses, cattails and buttonbush, 5% upland grassland, 5% along upland fence rows and 15% upland woods consisting largely of black oak. The opossum proceeded from one bare spot of ground to another in its search for food. This is typical. I have found that opossums seldom attempt to locate food beneath snow unless the snow blanket is less than about 5 cm in depth. These snow-free areas are usually located at the base of trees, logs and debris ("snow shadow", Pruitt 1960). At one point the opossum vigorously attacked the rotten underside of a log; beetle remains testified to its search for insects. On several occasions, it walked the full length of logs and wind-fallen tree limbs rather than in the snow. Twice there was evidence of coprophagy. The opossum crossed an open clearing and deliberately walked through a large brush pile and two rose thickets. For about 75 m, the animal walked on the ice in the middle of a small stream before crossing to the other side. Finally, the trail returned directly to the den. Thus, opossum trails are less haphazard than they may appear to be. In the process of investigating nooks which might hold food, the trail seems to wander. There is one strong impression I have obtained in following opossum trails. Opossums appear to be quite unsuccessful at capturing any of the homiotherms above ground in winter. Unlike foraging conditions in summer, young and helpless warm blooded prey are not available in winter. In view of the high incidence of warm blooded animals in the winter diet, it seems that many of these prey items must be obtained as carrion or captured alive in dens.

In summary, on a typical winter foraging trip, an opossum may find miscellaneous leavings such as scats, bones and fur of other carnivores, odd insects, berries and other plant items. On rare occasions it may come upon a bonanza in the form of a carcass. Success on these above-ground foraging trips appears to be highly variable, often extremely poor. Yet, even minute quantities of certain food items may provide essential nutrients such as trace minerals and vitamins which may reach a marginal level as much of the energy for winter survival is provided by tissue catabolism (see Chapters VIII and IX).

CHAPTER VI

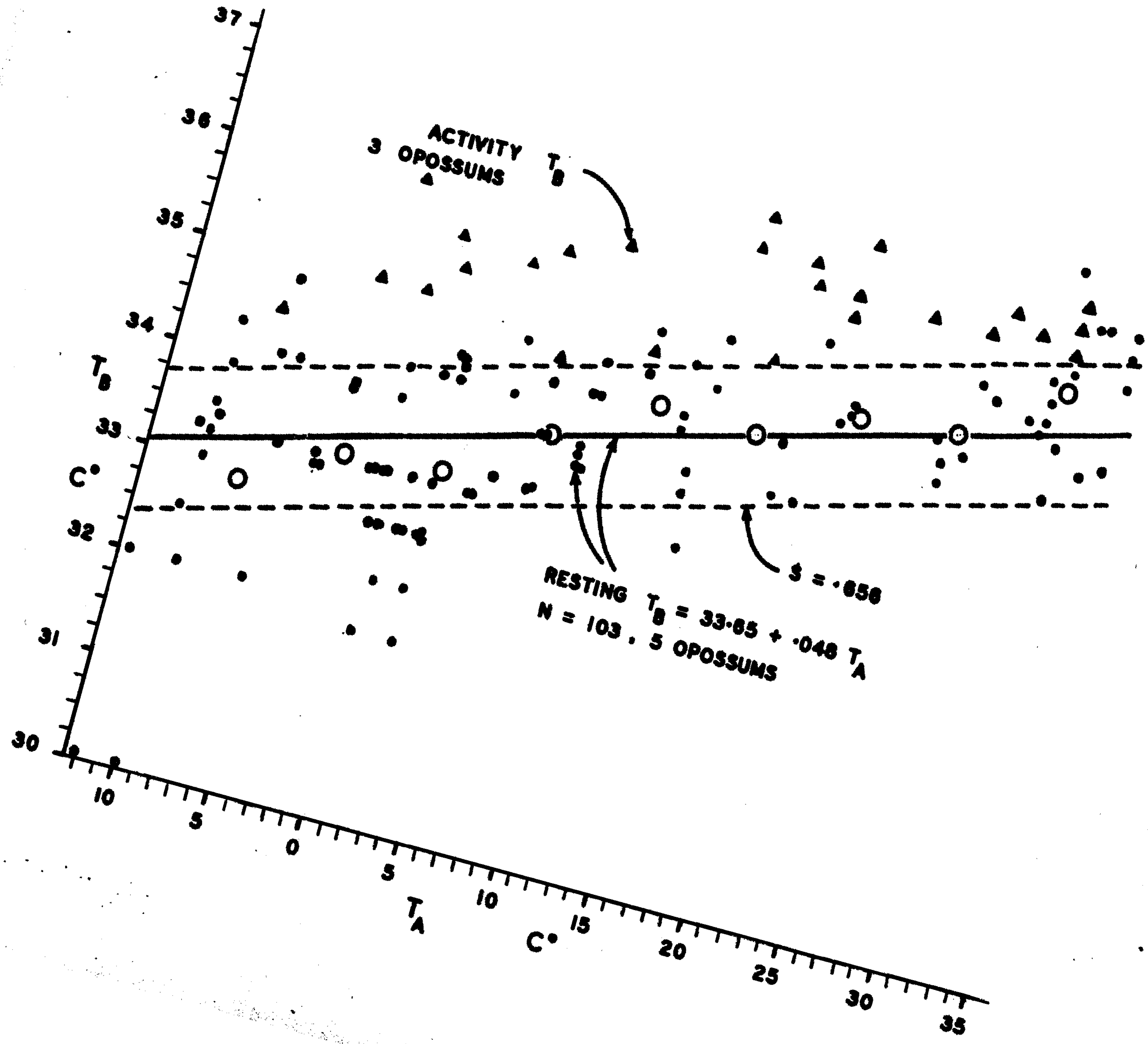
TEMPERATURE REGULATION

Body temperatures (T_B) of resting opossums plotted against ambient temperatures (T_A) show a linear relationship (Figure 14). The regression equation T_B (C^o) = 33.65 + 0.048 T_A was calculated from 103 observations on five animals by the method of least squares. The "t" test for the regression coefficient is significant ($p \leq 0.05$, Snedecor 1956). The resting T_B curve (Figure 14) shows a lability of 2.16°C over a T_A range of 47°C. On the basis of the regression equation, the T_B is 33.6°C at a T_A of 0°C and T_B equals T_A at an ambient temperature of 35.4°C. Greater variation in body temperature was displayed by individual animals. A large male (mean weight 4.79 kg) exhibited a T_B fo 32.0°C at T_A -12.0°C, and a T_B of 36.8°C at T_A 31.8°C. This is a T_B range of 4.8°C. A female (mean weight 2.73 kg) had a T_B of 29.8°C at T_A -10.0°C (the lowest value recorded in this study) and a T_B of 35.5°C at T_A 31.8°C, representing a range of 5.7°C for resting T_B. It should be noted that animals showed no signs of torpor at all T_A's and responded normally to stimuli at the lowest resting T_B values recorded here.

Body temperatures recorded during moderate activity (Figure 14) are one to three degrees higher than for resting animals. All activity values were obtained at night when animals were normally active. The difference between T_B's of active and resting animals is most pronounced at low ambient temperatures; this difference is only about 1°C or less at T_A 35°C (Figure 14). The data indicate that on those winter days when opossums are active for a few hours, their T_B 's would show an apparent diel cycle, being higher at night when animals are active. Comparison with Morrison's (1946) data for *Didelphis marsupialis etensis* is interesting. This tropical subspecies on Barro Colorado Island showed no diurnal T_B cycle. Body temperatures varied at random over a 2.5°C range, while the T_A's ranged from 24° to 29°C. Morrison's mean value for day and night T_B (50 measurements, two animals) is 35.5°C. Apparently the northern and tropical forms of *Didelphis marsupialis* differ little in the characteristics of their labile thermoregulation. The pronounced diel T_B range of the northern form during the cold months is probably an obligatory response to the greater difference between T_B and prevailing T_A's.

Scattered body temperature values are given by several investigators. These studies have been of short duration and under laboratory conditions. Johnson (1931) obtained five rectal temperatures from one animal ranging from 33.6°C to 35.5°C, with a T_A range of 25° to 29°C. This animal had a T_B varying from 33.5 to 34.7°C in a refrigerator

Figure 14. Opossum body temperatures (C^o) are plotted against ambient (environmental) temperatures for the period January through March, 1966. Hashed lines include one standard deviation on either side of the regression line.


ACTIVITY T_B
3 OPOSSUMS
RESTING $T_B = 33{\cdot}65 + {\cdot}048\ T_A$
N = 103 , 5 OPOSSUMS
$s = {\cdot}656$
T_B
C°
37
36
35
34
33
32
31
30
T_A
C°
10
5
0
5
10
15
20
25
30
35

(T_A 4° to 6°C). Wislocki (1933) obtained nine rectal temperatures ranging from 32° to 34.5°C at T_A 14° to 26°C. Britton and Atkinson (1938) state, "The opossum, Didelphia virginiana...showed practically no reduction in body temperature after exposure to approximately 0°C for several days."

Response of the opossum's body temperatures to controlled changes in ambient temperature have been studied by McManus (1969). His animals were kept outdoors at late summer temperatures (July, August and September). Rectal temperatures of these opossums remained essentially constant at approximately 35.5°C as the ambient chamber temperature was experimentally lowered to 3°C at the rate of 1°C every 6.8 minutes. McManus also recorded rectal temperatures at prevailing environmental temperatures of opossums kept outdoors during June, July, August, November and December. These measurements (interpreted from graph) show a slight drop in T_B of about 35.8°C at T_A 35.0°C, to about 34.8°C at T_A 5.0°C. The latter T_B measurements agree with those of this study (Figure 14) if the present activity and resting T_B values are lumped (McManus did not separate T_B measurements according to activity level).

The T_B measurements of McManus (1969) obtained at experimentally declining T_A's compared to T_B measurements of winter-acclimatized animals in the present study, illustrate the difference between acclimation, a short-term response and acclimatization, a long-term response.

Hart (1957) has discussed the importance of distinguishing between these thermoregulatory responses. The opossum apparently regulates quite precisely when it is subjected to short-term temperature changes, as the data of McManus show. However, the present data indicate that the opossum's thermoregulatory responses to seasonal changes in the environment are distinctly different from its short-term response. This is of considerable ecological importance. Significant energy savings can be atrributed to the opossum's lower resting T_B in the normal winter environment, as I will show in Chapter VII.

It is important that conditions are specified under which temperatures are recorded. These conditions include depth at which the T_B measurement was taken, ambient temperature, level of activity, length of acclimation, etc. Scott (1938) quotes rectal temperatures ranging from 32.0° to $37.1^{\circ}C$ in a laboratory with a T_A of 22° to 26° C. It is possible that Scott's values were recorded under varying conditions, e.g., the present study showed that depth of thermometer insertion is important. At a T_A ranging from -12° to $9^{\circ}C$, the mean of 20 T_B readings taken simultaneously at a depth of 3 cm is $31.39^{\circ}C$, an average of $1.89^{\circ}C$ lower than deep body readings. Again, it was found that T_B of fed animals was about $1^{\circ}C$ higher than for the fasting condition.

Low body temperatures and labile thermoregulation (i.e., imprecise thermoregulation) have been reported for other marsupials (Enders and Davis 1936, Morrison 1946, Bartholomew and Hudson 1962) and other mammals including monotremes (Martin 1903), pangolins (Eisentraut 1960), edentates (Wislocki and Enders 1935, Irving et al. 1942, Johansen 1961) and fossorial rodents (McNab 1966). Bartholomew (1956) measured the rectal temperature of the Australian marsupial Setonyx brachyurus, a small wallaby. He found that generally the T_B remained quite stable with most values between 37°C and 38°C. The T_B of two out of three animals declined to a low of about 36.5°C when the T_A was experimentally dropped from 20°C to 3°C and held at the lower value for four hours.

Most mammals with labile thermoregulation are tropical or subtropical forms. In the temperate environment, the opossum may exhibit the lowest normal body temperatures compared with other non-aestivating, non-hibernating mammals associated with it. Morrison and Ryser (1952) give a mean T_B of 38°C for 17 species (excluding monotremes, marsupials, edentates and bats) weighing from one to 10 kg. The mean T_B of 56 species weighing from 10 gm to 1000 kg is given as 37.8°C. These values are considerably higher than the opossum's body temperatures.

CHAPTER VII

ENERGY REQUIREMENTS BY OXYGEN CONSUMPTION

Resting oxygen consumption curves for four opossums are plotted in Figure 15. The equation for the line (fitted by eye) representing all data is: RMR (ml O_2/g/hr) = 0.51 - 0.014 T_A (C^o). Values calculated from the equation are given in Table 3. The general RMR line is projected to 35.4°C, the point of zero thermostatic heat requirement (where T_B equals T_A). The mean of 17 oxygen consumption values for slight to moderate activity (standing and slow movement) is 0.93 ml O_2/g/hr for three animals (s = 0.3). The latter measurements for moderate activity were made at a mean T_A if 5°C and a range in T_A of -4° to 11°C. The type of apparatus used here precluded metabolic measurements at higher activity levels.

The extremely low general BMR level is striking (Figure 15). A male (mean weight for the study was 4.79 kg) had a mean BMR of 0.15 ml O_2/g/hr (n = 22), at T_A's between 23.2°C and 28.6°C. A female (mean weight for the study was 2.73 kg) had a mean BMR of 0.16 ml O_2/g/hr (n = 19) at T_A 28.9°C. Basal metabolic rates of comparable, non-hibernating mammals are given in Table 4. It is apparent that the observed BMR values for the opossum are

Table 3. Resting oxygen consumption and metabolism calculated from the equation RMR (ml O_2/g/hr) = $0.51 - 0.014\ T_A$.

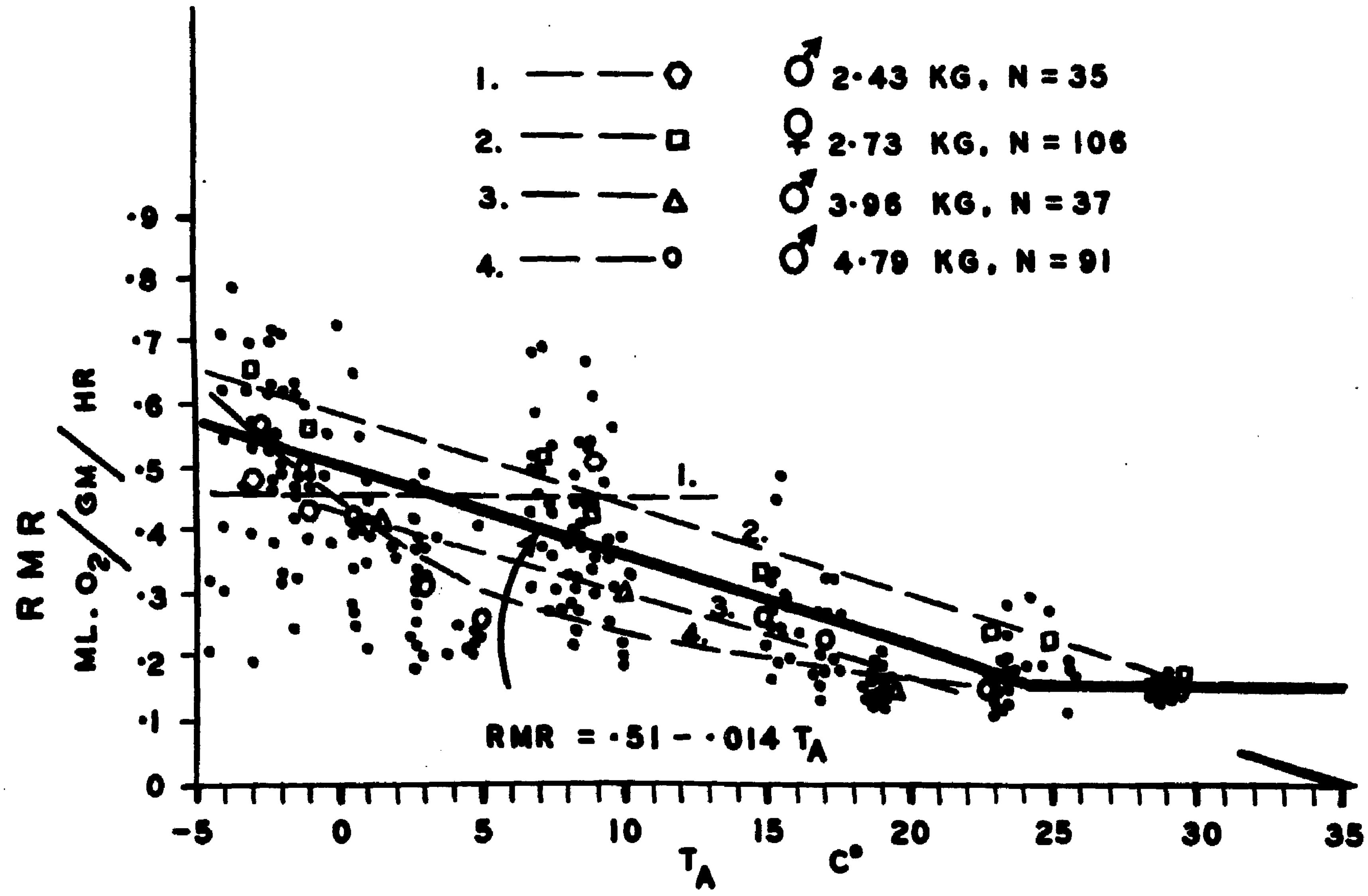
T_A	ml O_2/g/hr	kcal/kg/24 hrs.
-15	.73	84.09
-10	.65	74.88
-5	.58	66.81
0	.51	58.75
5	.44	50.69
10	.37	42.62
15	.29	33.41
20	.22	25.34
25	.15	17.28 Basal
30	.15	17.28 Basal

Table 4. Basal metabolic rates of some winter-acclimatized mammals. Calculated from Brody's (1945) equation: BMR (kcal/kg/24 hrs) = 70.5 wt. $(kg)^{-.27}$

Animal and Reference	Weight kg	Critical Temp. T_C °C	Observed[1] BMR kcal/kg/24 hrs	Observed BMR ml O_2/g/hr	Calculated BMR ml O_2/g/hr	BMR ratio Observed/ Calculated ml O_2/g/hr
Opossum, present study	4.79	21	16.81	.15	.40	.37
Opossum, present study	2.73	29	17.82	.16	.47	.34
Red Fox, Irving et al. 1955	5.01	-13	56.40	.50	.40	1.25
Arctic Fox, Scholander et al. 1950	5.50	-40	54.18	.58	.39	1.49
Arctic Fox, Scholander et al. 1950	4.60	-40	58.26	.52	.40	1.30
Arctic Fox, Scholander et al. 1950	4.00	-40	58.50	.52	.42	1.24
Porcupine, Irving et al. 1955	3.20	-12	50.76	.45	.45	1.00
Porcupine, Irving et al. 1955	6.70	-12	48.50	.43	.37	1.16
Porcupine, Irving et al. 1955	7.66	-12	38.35	.34	.35	.97

[1] 1 Liter oxygen is equivalent to 4.8 kcal.

Figure 15. Resting oxygen consumption versus ambient temperatures for fully acclimatized opossums. determined from January through July, 1966. Values to the left in the graph were collected in winter and values to the right in summer. Solid symbols represent oxygen consumption measurements. Open symbols represent mean values for the individual animals for two degree T_A classes. The four dashed lines have been fitted by eye to mean values for individual animals. The solid line is based on all data.


1.
2.
3.
4.
♂ 2·43 KG, N = 35
♀ 2·73 KG, N = 106
♂ 3·96 KG, N = 37
♂ 4·79 KG, N = 91
RMR
ML. O2/GM/HR
RMR = ·51 − ·014 TA
TA C°

less than 40% of the value predicted by Brody's (1945) equation relating BMR to body weight in mammals, where: BMR (kcal/kg/24 hrs) = 70.5 $wt(kg)^{-.27}$. The extremely low BMR of the opossum compares with 0.25 ml O_2/g/hr of the armadillo (mean weight 3.7 kg. Johansen 1961) and 0.13 ml O_2/g/hr of the three-toed sloth (mean weight 5 kg, Irving et al. 1942).

For any mammal with a relatively stable T_B, the RMR below the critical temperature may be described by the following equation (Kleiber 1961, Gordon et al. 1968):

$$RMR = (T_B - T_A)$$

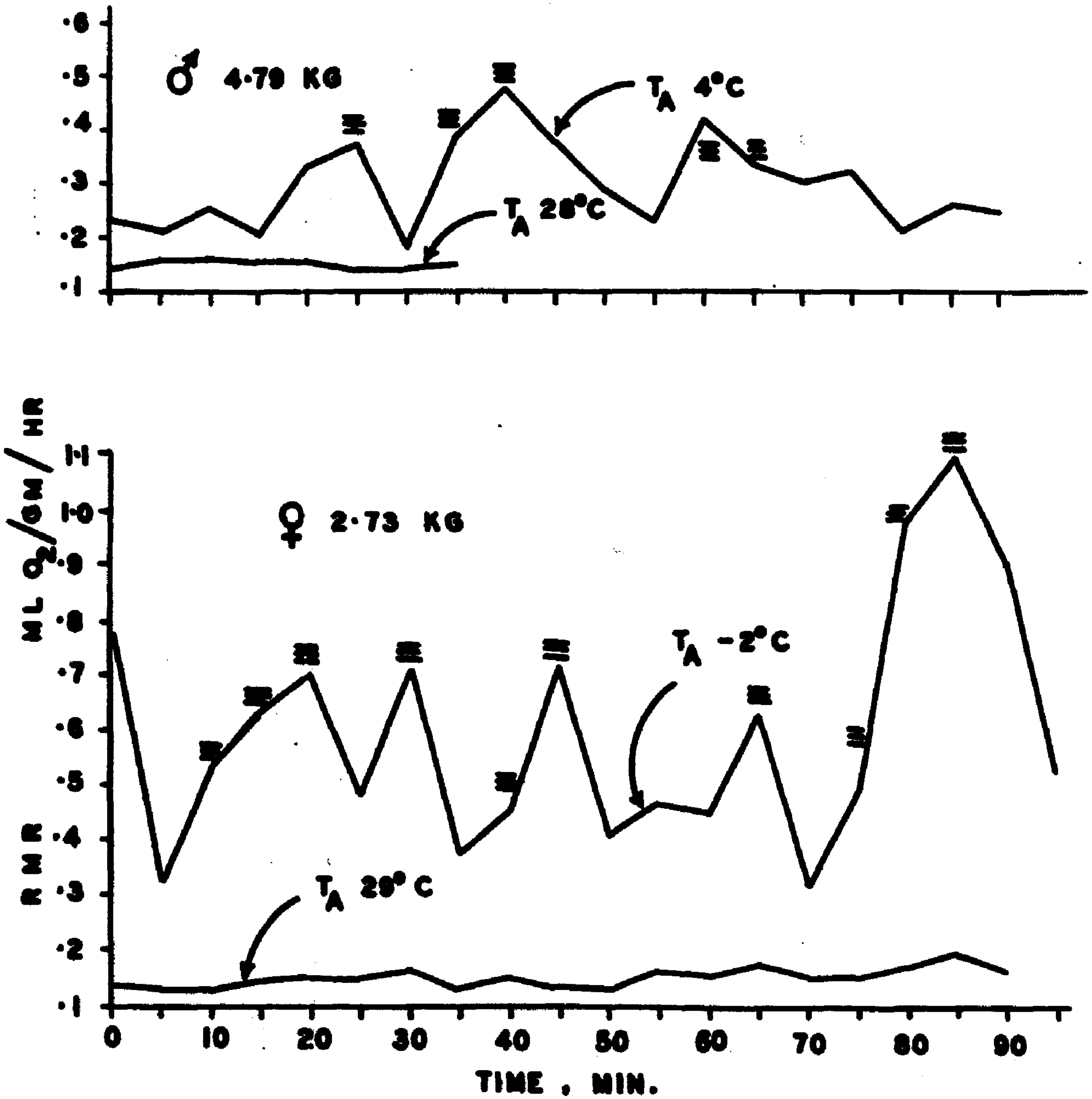
Where C, often called "conductance", is a constant equivalent to the rate of heat loss and is given by the slope of the line for RMR measurements at various T_A's. The value of C is a function of the temperature gradient maintained between T_B and T_A. However, for a labile homiotherm like the opossum, RMR is displaced downward from original proportionality as the T_B declines with declining T_A. Hence the value of C as obtained from the RMR line, which is 0.014 ml O_2/g/hr/$^{\circ}$C for the opossum (Figure 15), differs from C values calculated on the basis of actual temperature differentials maintained between T_B and T_A, at specified T_A's. For example, at T_A 25°C (the lower critical temperature, where T_B is 34.8°C) the value of C is 0.016 ml O_2/g/hr/$^{\circ}$C while at 0° (T_B 33.6°C), the value of C is .015 ml O_2/g/hr/$^{\circ}$C.

The opossum realizes some energy economy due to sliding T_B. If the opossum were to maintain a theoretical T_B of 35.4

in the manner of a rigid homiotherm, the energy cost would be greater by 8% of the normal energy cost above the basal level at T_A 0^oC (on the basis of data for all four animals, and C = 0.015 ml O_2/g/hr/^oC). In the case of the large male (4.79 kg), the equivalent energy savings is 12%. McNab (1966) reported a strong downward displacement of RMR (experimental T_A's) for the tropical mole-rat Heterocephalus glaber. He found that this tropical mammal shows remarkably poor thermoregulation, verging on poikilothermy. It is well known that homiotherms realize various levels of energy economy by a reduction of metabolic rate and associated T_B. Generally, the latter is a controlled response to specific stimuli. Such energy economy has been reported for torpid homiotherms (Pearson 1953, Lasiewski 1963, Hudson 1965, Tucker 1966 and others) and hibernating mammals (Kayser 1965 and others). Steen (1958) reported readjustment of T_B downward by small northern birds exposed to cold at night when they appeared unable to maintain their body temperature. Unlike these homiotherms, the opossum apparently achieves energy economy as an obligatory by-product of imprecise thermoregulation. The critical temperature (T_C) of the opossum is approximately 25^oC, a relatively high value for a temperate mammal. Yet, the opossum's rate of heat loss or energy expenditure at T_A 0^oC is comparable to that of a placental mammal with a BMR of 0.5 ml O_2/g/hr and a T_C of 0^oC (see Table 4 and Figure 15). In this connection, metabolic slopes of mammals with different BMR's have been graphically compared (Scholander 1950, 1955, Gordon et al. 1968 and others) by converting BMR to a common basal level (Basal 100 etc.). When the mammals being compared have widely different BMR's such comparisons will considerably distort relationships between metabolic rates. The energy cost at low T_A's of any mammal with a relatively high T_C and low BMR (like the opossum) will appear inflated.

A noteworthy aspect of opossum metabolism is the normal occurrence of shivering thermogenesis. Fluctuations in RMR below approximately 10°C are correlated with shivering (Figure 16). The regularity of shivering thermogenesis is astonishing. I have observed sleeping opossums showing alternate periods of shivering and quiet for hours at low T_A's. The comparative importance of shivering and non-shivering thermogenesis in mammals is presently not clear (Hemingway 1963). Apparently, with acclimation, placental mammals rely less on shivering and more on a non-shivering metabolic response to cold. Hemingway reviews evidence that shivering is an emergency mechanism and functions only in severe cold. In contrast to most northern mammals, shivering is employed frequently by winter acclimatized opossums, warranting consideration as a normal form of thermogenesis. Johansen (1961) reports the common occurrence of shivering among armadillos at low T_A's. Shivering and attendant increase in temperature were occasionally observed at a T_A of 30°C. (Johansen's armadillos were not acclimatized to experimental T_A's). West (1965) concludes that

Figure 16. Sequence of resting oxygen consumption measurements for two opossums, showing metabolic fluctuations associated with shivering at low T_A's. Dash marks represent shivering.



♂ 4·79 KG
T_A 4°C
T_A 28°C
♀ 2·73 KG
T_A -2°C
T_A 29° C
RMR ML O_2/GM/HR
TIME , MIN.

shivering and muscular activity are the principle means of extra heat production in birds. He found no evidence of non-shivering thermogenesis. While the evidence is meager, there is a hint that shivering thermogenesis may be the more primitive response.

In view of the decline in T_B with declining T_A, one would infer that a minimum T_A must exist below which a further decline in T_B places an intolerable physiological stress on the organism. The RMR shows increasingly wide fluctuations (Figure 16) as the T_A declines below $0^{\circ}C$. Winter sleeping opossums observed at T_A $-12^{\circ}C$ showed spells of deep breathing, much shivering and much shifting of positions. Evidence has been presented above that opossums avoid sub-freezing temperatures by utilizing the micro-environment of ground dens when the general air temperature declines below the freezing point. Hence, it appears that the "Achilles heel" of the opossum's unusual thermoregulatory-metabolic response is temperature sensitivity at a mean T_B below approximately $33^{\circ}C$ (at T_A $-5^{\circ}C$, the mean T_B is $33.41^{\circ}C$). Irving (1966) has reported a considerable internal temperature gradient from core to extremities in a number of species at low T_A's. At winter's end, many wild opossums display recently amputated ears and tails from freezing. This suggests difficulty in the maintenance of minimum temperatures in poorly insulated extremities. McManus (1969) measured rectal and tail temperatures of opossums subjected to ambient temperatures experimentally lowered to 3^{o}C. At T_A 3^{o}C, the T_B's in the tail, 12.7 cm (5 in.) and 20.3 cm (8 in.) from its base, were about 12^{o}C while the rectal temperature was 34.5^{o}C (values interpreted from graph). Thus, McManus' measurements indicate that the temperature gradient between T_B at the end of the tail and T_A was about 9^{o}C at T_A 3^{o}C.

From the standpoint of energy economy, the stable microclimate of the ground den with above-freezing T_A's is of pivotal importance. This is well illustrated by the oxygen consumption curve in Fugure 15. It has been previously noted that the resting energy expenditure of the opossum (Figure 15) does not exceed the basal energy expenditure (about .5 ml O_2/g/hr) of comparable cold-adapted mammals at T_A's of 0^{o}C or above. Representative BMR's (Table 4) of 0.55 ml O_2/g/hr for the arctic fox (Scholander et al. 1950), .50 ml O_2/g/hr for the red fox and .43 ml O_2/g/hr for the porcupine (Irving et al. 1955) are comparable to the opossum's RMR at 0^{o}C. The ecological importance of the opossum's use of ground dens can hardly be over-emphasized. For example, if the opossum were to sleep in a tree cavity at -15^{o}C (a situation it would not tolerate by choice), the oxygen consumption rate would increase to 0.7 ml O_2/g/hr, a 40% metabolic increase over the RMR level in a ground burrow at T_A 0^{o}C. For a 2.5 kg opossum, this metabolic increment per day is equivalent to 58 kcal, or in terms of prey, the energy provided by one additional field mouse each day.

The data presented here suggest that the opossum's unusual thermoregulatory-metabolic complex, coupled with its denning behavior, serve as an effective alternative to adaptive fur insulation. As Scholander (1955) has pointed out, insulation has been the main avenue for climatic adaptation in mammals. If indeed this alternative physiological response is as successful as it appears to be for the opossum, why is it such a rare phenomenon among temperate mammals? Perhaps the answer is that this adaptive response (particularly low metabolic rate) is necessarily associated with a low key mode of life for which the availability of accommodating ecological niches is limited. The almost universal occurrence of higher metabolic rates (excluding the special case of hibernation) and a T_B of about 38°C (Morrison and Ryser, 1952) for most mammals, suggest that these physiological characteristics confer to mammals a competitive advantage and a greater ability to extract energy from potential ecological niches.

CHAPTER VIII

ENERGY REQUIREMENTS BY FOOD BALANCE CALORIMETRY

Metabolizable Energy of Experimental Food

The designation "metabolizable energy" (M.E.) used here refers to the gross energy (combustion value for food) minus urinary and fecal energy. Energy values (kcal) of feces and urine of five opossums are given in Table 5. It will be noted that the dry and wet energy content of fecal material is quite similar for the five experimental animals. There is greater variation in the urinary energy between individuals, both in the wet and dry conditions. The relatively low energy value of wet urine for animal No. 5 is a consequence of the copious amount of urine produced by this individual.

The mean urinary energy value of 1.467 kcal/g dry weight may seem low compared to the mean value of 3.322 kcal/g dry weight reported for bobcat urine (Golley et al. 1965). However, the fraction of non-combustible material in the urine was high. For example, for animal No. 2, the mean weight of non-combustible residue in the urine comprised 54.12% of the total weight (n = 5, range = 54.16 - 54.36%). The combustion value of the ash-free dry material averaged 3.248 kcal/g which is higher than the calculated

Table 5. Energy values (kcal) determined by bomb calorimeter for feces and urine of opossums on a maintenance diet in autumn.

Opossum No. and Sex		Mean Weight	Fecal Energy Content dry kcal/g	Fecal Energy Content wet kcal/g	Urinary Energy Content dry kcal/g	Urinary Energy Content wet kcal/g
1	♀	3.03	3.311	1.120	1.207	.025
2	♀	3.45	3.307	1.359	1.477	.040
5	♂	2.44	3.439	1.124	1.212	.014
9	♀	3.29	3.538	1.369	1.607	.046
10	♂	2.01	3.585	1.341	1.830	.047
Mean		2.84	3.436	1.263	1.467	.034

combustion values for urea (2.52 kcal/g) and uric acid (2.74 kcal/g) containing the major energy fraction in mammalian urine.

The energy value of the kibbled dog food used in the winter food balance energy determinations is 4.010 kcal/g. The energy value of the dog food batch used to calculate energy values in Table 7 is 4.220 kcal/g. These values are slightly lower than 4.365 kcal/g quoted by the Ralston Purina Company (personal communication, Corbin, 1968).

The food intake and excretory output of opossums on a maintenance diet is given in Table 6. These values and the values from Table 5 were used to calculate energy intake, excretory energy loss and metabolizable energy, which are given in Table 7. The high variability of fecal output of animal No. 2 (Table 6) is due to the fact that this animal defecated every second day and output is expressed on a daily basis. When animals are compared, gross and metabolizable energy requirements and excretory energy loss per unit body weight, increase with decreasing body weight (Table 7) as might be expected with the increase in ratio of surface area to body weight as the weight declines (proportional to $W^{.75}$, Kleiber 1961). However, it is interesting to note that per animal, the gross and metabolizable energy requirements and excretory energy loss are similar for all five animals (Table 7). The latter effect is predictable because the decrease in metabolic rate due to the decrease in total body size (or weight) tends to be

Table 6. Food intake and excretory output of opossums on a maintenance diet in autumn. Mean values are given plus or minus one standard deviation.

Opossum No. and Sex		Days of Experiment	Mean Weight (kg)	Mean Food Intake Per Animal (g/day)	Food Intake Per Unit Body Wt. (g/kg/day)	Feces Output Per Animal (Wet) (g/day)	Feces Output Per Unit Body Wt. (g/kg/day)	Urine Output Per Animal (ml/kg/day)	Urine Output Per Unit Body Wt. (ml/kg/day)
1	♀	15	3.03	65.0	21.4	28.9 ± 19.1	9.5 ± 6.3	64.4 ± 23.9	21.2 ± 7.9
2	♀	15	3.45	65.0	18.8	28.1 ± 28.6	8.1 ± 8.3	100.5 ± 17.7	29.1 ± 5.1
5	♂	15	2.44	65.0	26.6	34.9 ± 12.0	14.3 ± 4.9	218.0 ± 61.0	89.3 ± 25.0
9	♀	21	3.29	65.7	20.0	35.5 ± 9.7	10.8 ± 2.9	85.1 ± 24.8	25.9 ± 7.5
10	♂	21	2.01	60.0	29.8	30.5 ± 14.0	15.2 ± 7.0	73.5 ± 32.7	36.6 ± 16.3
Means (n = 5)		17.4	2.84	64.1	22.5	31.6	11.1	108.3	38.1

Table 7. Energy intake, excretory energy loss and metabolizable energy of opossums on a maintenance diet in autumn.

Opossum No. and Sex		Mean Weight (kg)	Gross Energy Intake Per Animal (kcal/day)	Gross Energy Intake Per Unit Body Wt. (kcal/kg/day)	Fecal Energy Per Animal (kcal/day)	Fecal Energy Per Unit Body Wt. (kcal/kg/day)	Urinary Energy Per Animal (kcal/day)	Urinary Energy Per Unit Body Wt. (kcal/kg/day)	M.E. Per Animal Per Day (kcal/day)	M.E. Per Unit Body Wt. Per Day (kcal/kg/day)	M.E. as % Energy Intake
1	♀	3.03	260.65	86.02	32.37	10.68	1.63	.54	226.65	74.80	86.95
2	♀	3.45	260.65	75.55	38.19	11.07	4.02	1.16	218.44	63.32	83.80
5	♂	2.44	260.65	106.82	39.23	16.08	3.05	1.25	218.37	89.49	83.78
9	♀	3.29	277.25	84.27	48.60	14.77	3.91	1.19	224.74	68.31	81.06
10	♂	2.01	253.20	125.97	40.90	20.35	3.45	1.72	208.85	103.90	82.48
Mean		2.84	262.48	95.73	39.86	14.59	3.21	1.17	219.41	79.96	83.61

compensated by an increase in metabolic rate due to the greater surface area to weight ratio in smaller animals.

The efficiency of dog food in terms of metabolizable energy is given in Table 7. These values do not deviate more than 3.34% from the mean of 83.61% for all five animals. For the bobcat, Golley et al. (1965) report that the fraction of metabolizable energy as percent of energy intake ranged from 79% to 82% for three animals which did not gain weight. These values are quite similar to those determined here, even though the diet of bobcats was deer meat. Other M.E. fractions for bobcats which gained weight on a rabbit and chicken diet (Golley et al. 1965) ranged from 61% to 84%.

Maximum Energy Intake

An estimate of maximum energy intake per day was required for calculating the winter energetics models in Chapter X. Forty-three feeding trials were conducted. Dead cottontail rabbits were fed ad libitum to caged opossums in winter. Usually, a 1.5 kg rabbit was consumed by an opossum in three or four nights. Rabbits were almost completely consumed in all cases. Often, the only remnants were the distal portion of a leg or piece of fur.

Opossums attacked carcasses with avidity. Their strong jaws opened carcasses at almost any point, often at the ventral posterior end. Body juices were licked out; forepaws were used for grasping and holding. Sometimes the head was eaten first. On one occasion, smelt was offered to a 3.0 kg female. She ate 531 g of smelt in one night (value not included here). The results are given in Table 8.

Table 8. Ad libitum daily ingestion of whole rabbit by opossums in winter. The mean weight of rabbit ingested is given plus or minus one standard deviation.

Body wt. of opossum (kg)	No. of feeding trials (days)	Mean wt. of rabbit ingestion(g)	Mean wt. of whole rabbit ingested per unit body wt. g/kg/day
2.10 ♂	9	238 ± 41.8	113.3
2.50 ♂	9	337 ± 46.1	134.8
3.00 ♀	13	355 ± 97.8	118.3
4.20 ♂	12	467 ± 97.7	111.2
	n = 43		119.4

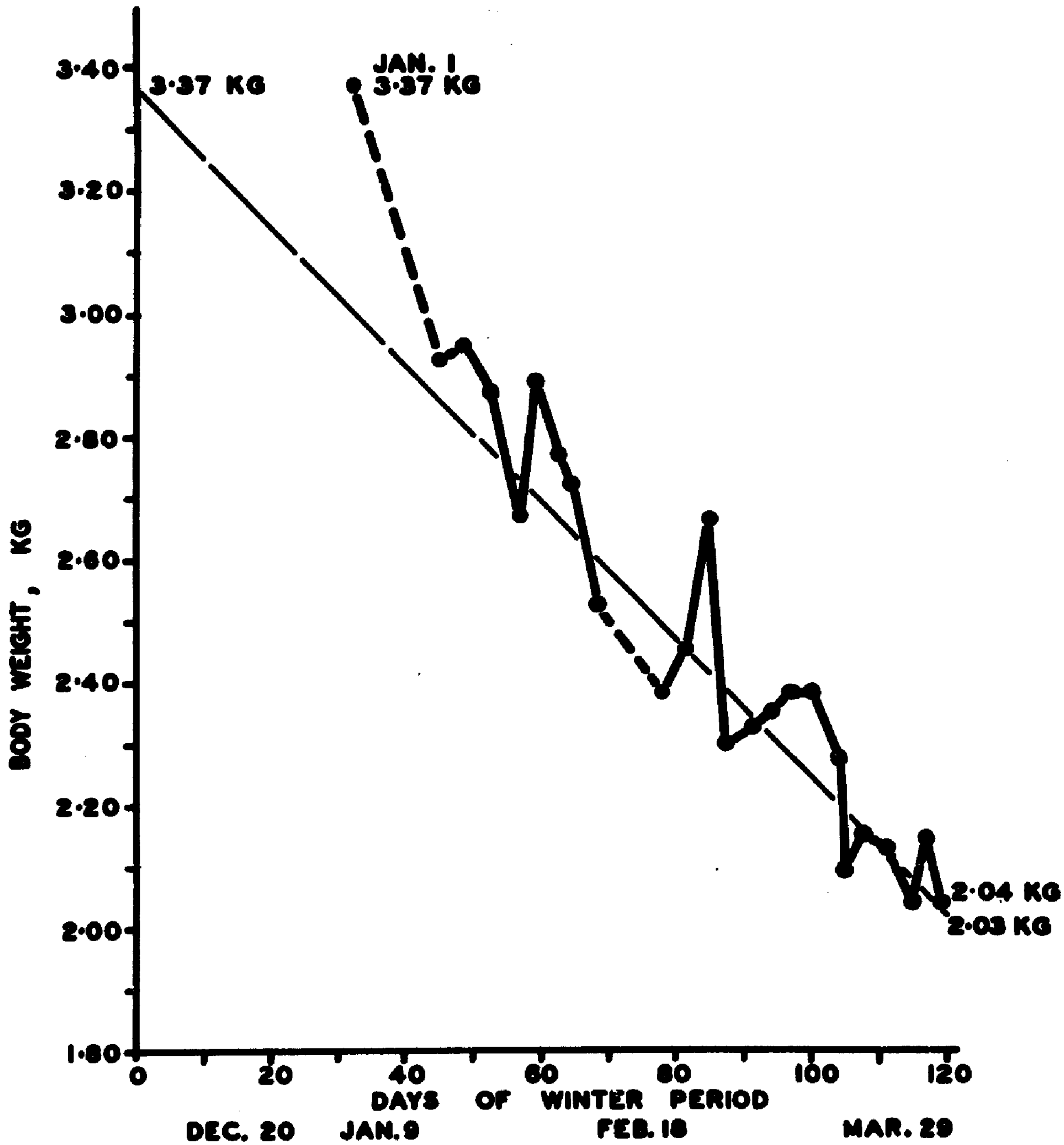
Assuming (Table 8) that 120 g rabbit flesh can be ingested per kg of opossum weight in one day and the combustion value of whole rabbit is the same as Microtus (1.37 kcal/g wet weight, Golley 1960), then the gross energy value of 120 g rabbit/kg opossum (Table 8) is 164.4 kcal. Assuming a value of 80% as the efficiency of conversion from gross energy to metabolizable energy (Table 7 and Golley et al.'s data, 1965), then the maximum daily M.E. intake for an opossum is 131 kcal/kg body weight. For a 2.4 kg opossum (the mean winter weight of 154 road-killed opossums) the maximum daily M.E. intake in winter is 314.4 kcal, or 315 kcal as a round number.

Energy Requirements for Sleeping and Activity in Winter

Examples of decline in body weight of three experimental opossums are shown in Figures 17, 18 and 19. Opossum No. 5 (Figure 17) and No. 2 (Figure 18) were introduced into the experimental pens on January 1. Until January 1, feeding had been ad libitum and the animals were very fat. In each case, the body weight in January was assumed to be the weight at the start of the hypothetical winter period of 120 days (Figure 17) which was December 1, the period ending on March 29. It seemed desirable to mimic the winter weight loss rate of wild opossums in the weight loss of experimental animals. In the wild, opossums may lose as much as 40% or slightly more of their body weight over the winter period (data presented in Chapter IX) which is equivalent to a daily weight loss rate of .33% of the initial winter weight. The latter weight loss rate was used as a guideline (Figures 17, 18, 19) and I tried to adjust the feeding rate so that the body weight followed this guideline as closely as possible. The 40% weight loss rate was maintained through February 16. After February 16, an attempt was made to maintain body weight at constant level for all animals to measure the maintenance energy requirment at various activity levels. Opossum No. 7 (Figure 19) was captured in the wild on January 20 and the initial winter weight was calculated on the assumption that weight loss had proceeded at the daily rate of .33% of the initial winter weight. This animal died of starvation on March 14, as was noted previously.

Figure 17. The decline in body weight of a typical experimental opossum (No. 5, ♂) during the period fro January 1 to March 29, 1968. Weight decline is represented by the heavy line. The dashed portions of the heavy line represent weight decline during periods when the opossum did not emerge from the den. The light dashed line represents theoretical weight loss over the 120 day winter period at the daily rate of .33% of the initial winter weight (on Day 1 or Dec. 1) equivalent to a total weight loss of 40% of the initial winter weight over the 120 day winter period (see text).* The latter line was used to guide the experimental weight loss rate through February 16. Maintenance energy requirement was measured after February 16.

* The latter line was used to guide experimental weight loss rate through February 16.



3·40
3·20
3·00
2·80
2·60
2·40
2·20
2·00
1·80
BODY WEIGHT, KG
3·37 KG
JAN. 1
3·37 KG
2·04 KG
2·03 KG
0
20
40
60
80
100
120
DAYS OF WINTER PERIOD
DEC. 20
JAN. 9
FEB. 18
MAR. 29

Figure 18. The decline in body weight of an experimental opossum (No. 2, ♀) during the period from January 1 to March 29, 1968. Weight decline is represented by the heavy line. The dashed portions of the heavy line represent weight decline during periods when the opossum did not emerge from the den. The light dashed line represents theoretical weight loss over the 120 day winter period at the daily rate of .33% of the initial winter weight (on Day 1, or December 1), equivalent to a total weight loss of 40% of the initial winter weight over the 120 day winter period (see text).* Maintenance energy requirement was measured after February 16.

* The latter line was used to guide experimental weight loss rate through February 16.

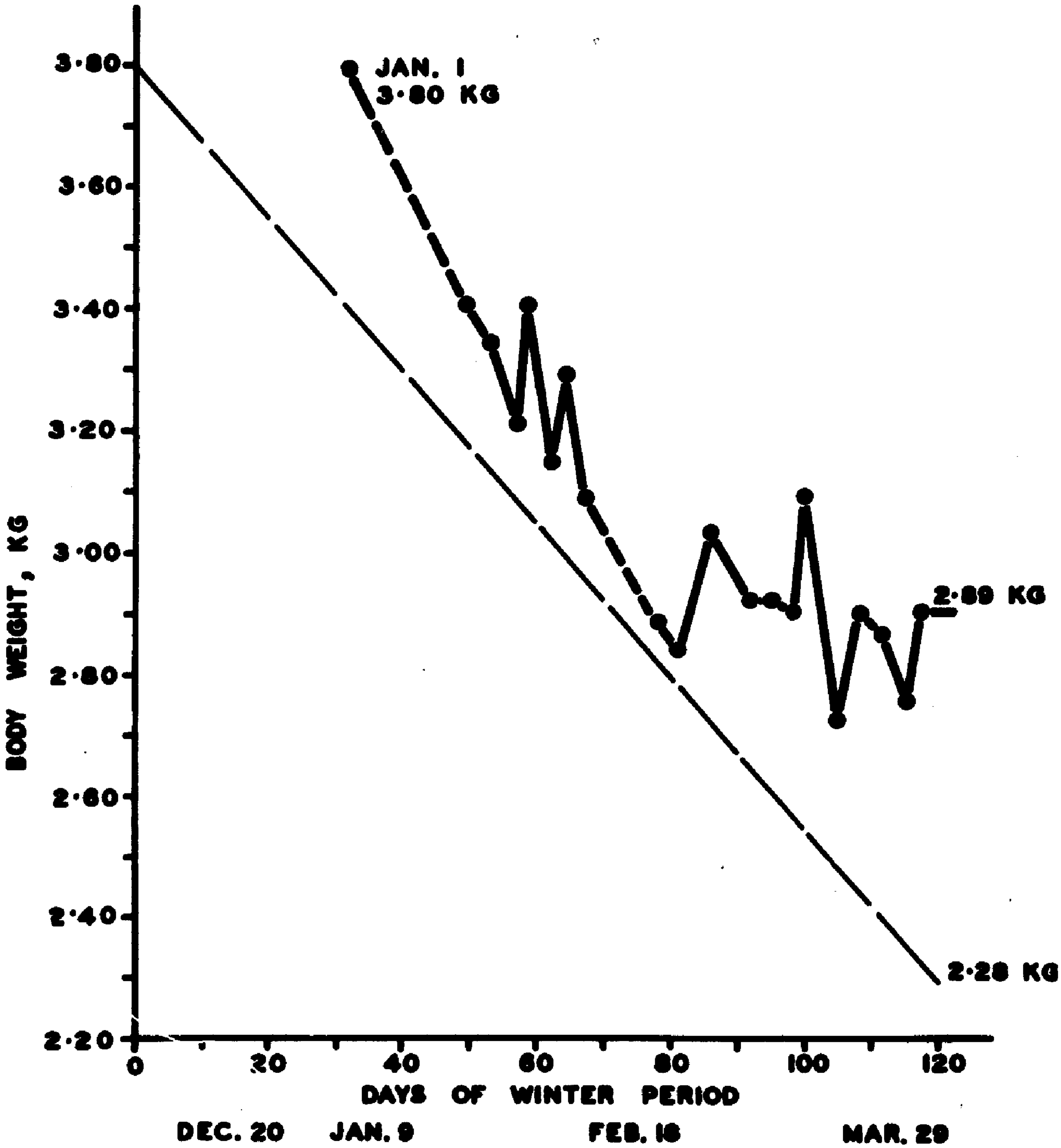
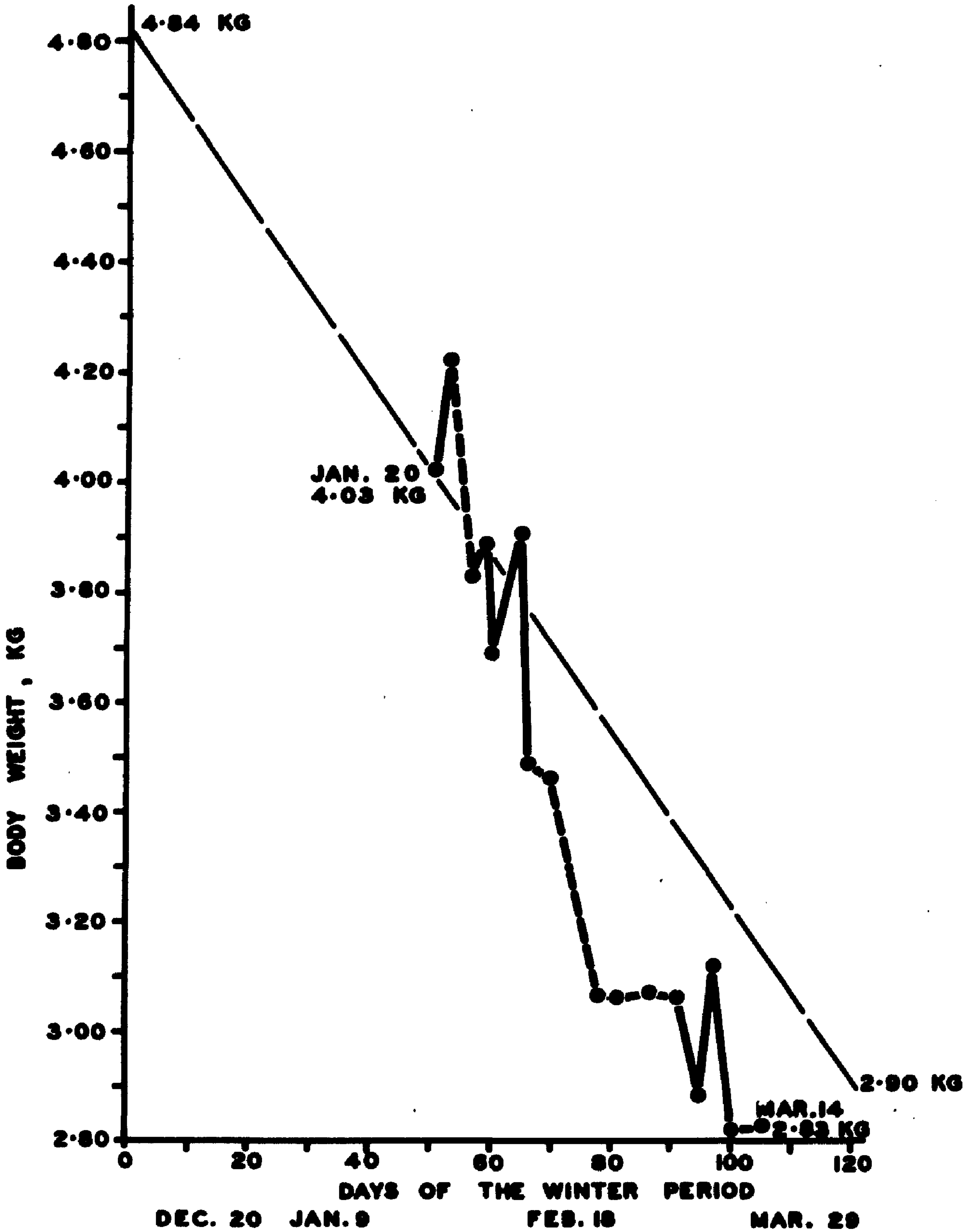

JAN. 1
3·80 KG
2·89 KG
2·28 KG
3·80
3·60
3·40
3·20
3·00
2·80
2·60
2·40
2·20
BODY WEIGHT, KG
0
20
40
60
80
100
120
DAYS OF WINTER PERIOD
DEC. 20
JAN. 9
FEB. 16
MAR. 29

Figure 19. The decline in body weight of an experimental opossum which failed to survive (No. 7, ♂), during the period from January 20 to March 14, 1968. Weight decline is represented by the heavy line. The dashed portions of the heavy line represent weight decline during periods when the opossum did not emerge from the den. The light dashed line represents theoretical weight loss over the 120 day winter period at the daily rate of .33% of the initial winter weight, equivalent to a weight loss of 40% of the initial calculated winter weight (on Day 1 or December 1) over the 120 day winter period (see text). The latter line was used to guide the experimental weight loss rate through February 16. Maintenance energy requirement was measured after February 16 (see text). This animal died of starvation on March 14.


4·84 KG
JAN. 20
4·03 KG
MAR.14
2·83 KG
2·90 KG
BODY WEIGHT, KG
4·80
4·60
4·40
4·20
4·00
3·80
3·60
3·40
3·20
3·00
2·80
0
20
40
60
80
100
120
DAYS OF THE WINTER PERIOD
DEC. 20
JAN. 9
FEB. 18
MAR. 29

The M.E. requirement was calculated for various periods after February 16 during which body weight was maintained at constant or near constant level. By knowing the weight of food consumed and the efficiency of conversion of food to metabolizable energy (Table 7) the energy expenditure rate was calculated for various measurement periods in winter. An example of data used to calculate maintenance energy requirement is given in Table 22, Appendix A. These results are given in Tables 9 and 10.

The lowest rates of metabolism corresponding to periods of minimum activity, primarily at the probing level, and maximum sleep are given in Table 9. The mean M.E. expenditure for seven animals is 1.96 kcal/kg/hr, or 112 kcal/24 hrs at the mean body weight of 2.38 kg. This value is lower than the B.M.R. predicted by either Brody's (1945) or Kleiber's (1961) equations. On the basis of Kleiber's equation:

$$\text{B.M.R. (kcal/24 hrs)} = 70\ w(\text{kg})^{.75}$$

A mammal weighing 2.4 kg has a basal metabolic rate of 135 kcal/24 hrs, a value higher than the equivalent one of 112 kcal for the opossum. Conversely, the opossum's mean metabolic rate of 112 kcal/24 hrs is equivalent to the equation:

$$\text{M.R.(kcal/24 hrs)} = 58\ w(\text{kg})^{.75}$$

It is evident that the lesser factor of 58 compared to the interspecific value of 70 reflects the opossum's lower metabolic rate.

Table 9. Metabolizable energy (M.E.) requirements of opossums for sleeping and minimum activity in winter.

Opossum Number and Sex		Body Weight kg	Measurement Period	Days	Rate M.E. Expenditure for Period kcal/kg/hr	Mean Activity Span hrs/night	Mean Activity Intensity units/hr
1	♀	1.82	Feb. 24 - Mar. 2	8	2.36	6.0	2.9
2	♀	2.92	Feb. 29 - Mar. 3	4	1.44	6.0	1.9
3	♀	2.08	Feb. 29 - Mar. 3	4	2.03	6.0	2.8
4	♀	2.27	Feb. 5 - 23	18	1.95	-	-
5	♂	2.28	Feb. 16 - 24	9	1.94	7.8	6.5
6	♂	2.24	Feb. 24 - Mar. 5	11	2.09	7.1	2.7
7	♂	3.06	Feb. 16 - 28	13	1.92	3.1	3.0
Mean		2.38		9.6	1.96	6.0	3.3

Table 10. Metabolizable energy (M.E.) requirements of opossums for periods at differing activity levels. Mean values are underlined.

Opossum Number and Sex		Body Weight kg	Measurement Period	Days	Rate M.E. Expenditure for Period kcal/kg/hr	Mean Activity Span Hrs/Night	Mean Activity Intensity Units/hr
1	♀	1.76	Mar. 9 - 16	8	2.58	8.7	3.7
		1.76	Mar. 9 - 27	19	3.21	9.3	3.7
		1.73	Mar. 20 - Apr. 2	14	3.84	8.8	3.1
		1.75			3.21		
2	♀	2.89	Mar. 7 - 16	10	1.55	8.1	3.5
		2.89	Mar. 17 - 25	9	2.15	8.7	2.5
		2.89	Mar. 26 - 30	5	2.71	8.0	2.2
		2.89			2.14		
3	♀	2.07	Mar. 4 - 16	13	2.23	6.9	3.2
		2.07	Mar. 17 - 23	7	2.40	8.3	3.3
		2.07	Mar. 24 - 30	7	3.75	10.3	2.5
		2.07			2.79		
4	♀	2.04	Feb. 19 - 28	10	3.08	6.5	2.6
		2.04	Feb. 29 - Mar. 2	3	3.43	5.7	3.7
		2.08	Mar. 9 - 13	5	2.75	4.8	3.7
		2.05			3.09		
5	♂	2.38	Feb. 16 - 24	9	2.61	6.4	3.5
		2.15	Mar. 17 - 25	9	2.89	10.9	7.3
		2.04	Mar. 24 - Apr. 2	10	4.05	10.8	13.5
		2.19			3.18		
6	♂	2.13	Feb. 16 - 28	13	2.52	5.9	2.7
7	♂	3.08	Feb. 24 - Mar. 5	11	2.88	6.7	3.6
		2.82	Mar. 8 - 12	5	2.28	11.2	7.0
		2.95			2.58		
8	♂	1.84	Mar. 24 - 30	7	4.66	10.1	3.5
Means (n = 19)		2.25			2.92	8.2	4.1

An equation for opossum B.M.R. can be calculated from the oxygen consumption data. The mean weight of the four animals used in oxygen consumption measurements was 3.48 kg. The basal energy expenditure at the latter weight is 60.2 kcal/24 hrs (see data given under oxygen consumption). On this basis, the equation for opossum B.M.R. becomes:

$$\text{Opossum B.M.R. (kcal/24 hrs)} = 23.6\ W(\text{kg})^{.75}$$

The factor of 23.6 is probably among the lowest for mammals!

Agreement between energy expenditure estimates of sleeping opossums by food balance calorimetry and by oxygen consumption is good. Using the equation for oxygen consumption; R.M.R. (ml/g/hr) = 0.51 - 0.014 T_A (C^o), and assuming 4.8 kcal/l of oxygen consumed at a mean body weight of 2.38 kg and a mean winter temperature for ground dens of 2.2^{o}C, the energy expenditure estimate by oxygen consumption is 2.3 kcal/kg/hr. The equivalent estimate by food balance is 1.96 kcal/kg/hr for a mean body weight of 2.38 kg, as given in Table 9.

Energy requirements for higher activity levels are given in Table 10. It is evident that the M. E. values vary widely between and within measurements for various individuals. There is some correlation with mean activity intensity measured by switch closures at ground and tree den entrances. However, the correlatior is poor.

Energy Equivalent of Body Weight Loss

The energy equivalents of body weight loss are given in Table 11. Energy equivalents were calculated from minimum M.E. rates measured for individual animals (Table 9) applied to their known weight losses during periods when these animals stayed in their dens continuously. The mean M.E. value for seven animals is 4.38 kcal/g weight lost; the range is 3.03 to 5.35 kcal/g weight loss (Table 11). If the mean value of 4.4 kcal/g weight loss approximates the true value, then a considerable amount of moisture must comprise the weight loss in opossums. Brown et al. (1951) report values for high density belly fat of swine as follows: ether extract 63.36%, protein 8.59%, moisture 27.76%, and ash .37%. On this basis, assuming a ratio of:

$$\frac{\text{Protein}}{\text{Fat}} = \frac{1}{7}\ ;$$

for composition of weight loss, and the combustion value for lipid is 9.5 kcal/g, and the combustion value for protein is 5.6 kcal/g, (Brody 1945) then to produce an energy value of 4.4 kcal/g of weight lost, approximately 42% of the weight lost is lipid, 6% is protein and 52% is moisture and ash.

Energy Requirements Concurrent with a Body Weight Loss of 40%

The M.E. expended while opossums were losing weight at the daily rate of .33% of the initial winter weight, or a total weight loss of 40% during the 120 day winter period, is given in Table 12. Measurement periods were established

Table 11. The metabolizable energy (M.E.) equivalent of weight loss while opossums were in the dens in winter. Most of the time was spent in sleep. The minimum M.E. expenditure rate for each animal was used in calculations (see Table 5).

Opossum Number	and Sex	Measurement Period	Days	Mean Weight for Period kg	Weight Decline for Period gs/day	M.E. rate used in Calculations kcal/kg/hr	M.E. kcal/g weight loss
1	♀	Jan. 2 - 18	17	2.68	28.3	2.36	5.35
2	♀	Jan. 2 - 18	17	3.60	23.4	1.44	5.31
3	♀	Jan. 2 - 13	12	3.17	37.5	2.03	4.11
4	♀	Jan. 5 - 17	13	2.89	39.2	1.95	3.44
5	♂	Jan. 2 - 14	13	3.14	34.6	1.94	4.22
6	♂	Feb. 5 - 15	11	2.21	21.3	2.09	5.20
7	♂	Feb. 8 - 15	8	3.26	49.5	1.92	3.03
		Mean (n = 7)	13	2.99	33.4	1.96	4.38

Table 12. Metabolizable energy (M.E.) expended and percentages of M.E. derived from food and loss of body substance, while opossums were losing weight at the approximate daily rate of .33% of the initial winter weight, equivalent to a total weight loss of 40% of the initial winter weight over the 120 day winter period.

Opossum Number and Sex	Mean Body Weight kg	Measurement Period	Days in Period	Total kcal for Period	Metabolizable Energy Expended: From Loss of Body Substance %	From Food %	kcal/day	kcal/$\bar{x}$ kg Body wt/day
1 ♀	2.09	Jan. 18 - Mar. 28	70	10,329	35.7	64.3	147	70.6
2 ♀	3.36	Jan. 1 - Mar. 4	63	8,167	57.2	42.8	130	38.6
3 ♀	2.54	Jan. 13 - Mar. 26	73	8,321	40.5	59.5	114	44.9
4 ♀	2.36	Jan. 18 - Mar. 3	46	6,700	28.7	71.3	146	61.9
5 ♂	2.66	Jan. 17 - Mar. 9	52	7,143	33.7	66.3	137	51.5
6 ♂	2.31	Jan. 22 - Feb. 28	38	4,634	39.3	60.7	122	52.8
7 ♂	3.40	Jan. 31 - Mar. 6	35	5,899	29.1	70.9	168	49.4
Mean	2.67		54	7,313	37.7	62.3	137.7	52.8

by selecting dates in the winter period between which weight loss occurred at the rate of 40%. The total energy expenditure in Table 12 was calculated by adding the energy equivalent of the food eaten to the energy equivalent for weight lost by each individual (the latter based on values in Table 11).

It appears that approximately 38% of the opossums total winter energy is provided by catabolism of body tissue and 62% by food (Table 12). In neat fractions, approximately one-third of the winter energy is provided by body substance and two-thirds by food. A simple approximation of winter energy expenditure can be calculated using means in Tables 9 and 12. Assuming that the mean weight of hypothetical opossum is 2.7 kg with a mean energy expenditure of 53 kcal/kg/day, then the daily energy expenditure is 143 kcal and the total winter energy expenditure is 17,160 kcal. If 38% of the energy is provided by body tissue, then the tissue alone provides energy for 46 days if the energy expended is identical on all winter days (which it is not). However, the fat tissue will sustain the animal longer if it is sleeping in the den. If a minimum metabolic rate of 1.87 kcal/kg/hr is assumed (mean value from Table 9, eliminating the two lightest animals, No. 1 and No. 3), then the daily energy expenditure for an opossum of 2.7 kg is 121.2 kcal/24 hrs. The fraction of total energy provided by tissue catabolism is .38 x 17,160 = 6521 kcal, or at the rate of 121.2 kcal/24 hrs, catabolism of tissue would sustain the animal for 54 days in the den.

CHAPTER IX

DECLINE IN BODY WEIGHT AND FAT IN WILD OPOSSUMS

The accuracy of the specific gravity technique depends on the density estimates for fat and lean portions of an animal body. The following fat density values are reported by various workers: .918 g/cc for human (Behnke et al. 1942), .912 for guinea pigs (Morales et al. 1945), .948 to .995 for swine depending on protein and moisture content (Brown et al. 1951), .892 for cattle (Kraybill et al. 1951) and .94 for beef and mutton tallow (Hodgeman et al. 1964). In this study, the fat density value of .912 was used in calculations.

Initial calculations were based on a density estimate for the lean portion of the carcass derived from published values. This value had to be revised. Behnke et al. (1942) carefully estimated a density of 1.095 for the fat-free portion of the human body. Subsequently, a number of workers have used the latter figure rounded off to 1.10 to represent the lean portion of carcasses (Rathbun and Pace 1945, Morales et al. 1945, Kraybill et al. 1951, 1953). In this study, the specific gravity of some of the animals was found to be greater than 1.10. One male which died of starvation in the experimental pens had a specific gravity of 1.102.

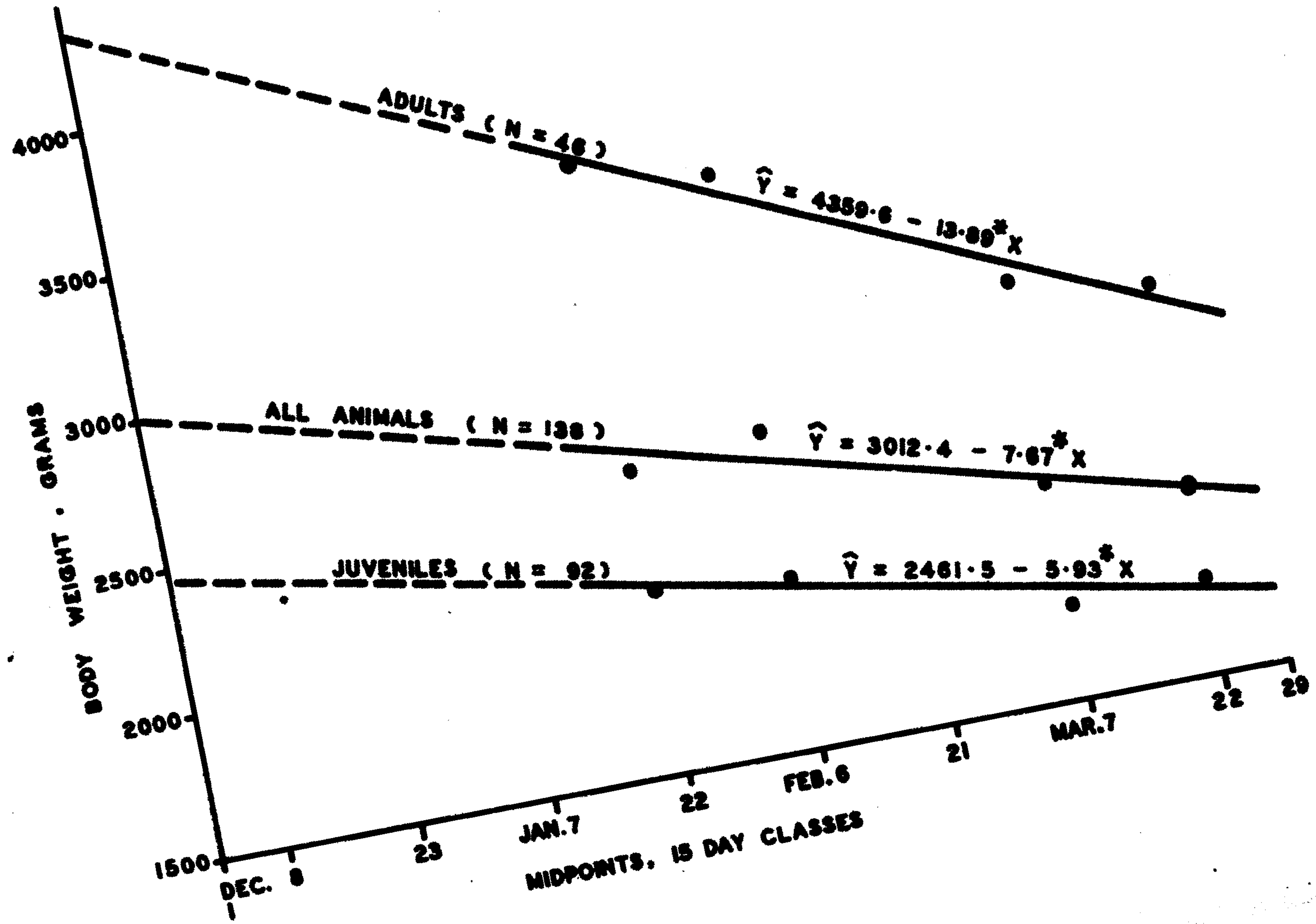
The other high density values were 1.102, 1.107 and 1.108 from emaciated, road-killed specimens. If the density value of 1.10 is used to calculate percent fat in the latter animals, a fat value less than zero is obtained. Actually, some fat remains even in starved animals. The lipid remnant is apparently an integral part of cell structure (Keys et al. 1950). Fat remaining in starved animals has been reported as 2.3 to 2.5% for mice (Terroine et al. 1922), 5.5% for rats (Reed et al. 1930) and 1.9% for cattle (Trowbridge et al. 1918). In this study, the following formula was used (see Appendix A, formula derived from the theoretical formula of Kraybill et al. 1953) based on a density value of 1.11 for lean:

$$\text{Percent opossum fat} = 100 \quad \frac{5.111}{\text{Spec. Grav.}} \quad - 4.606$$

This formula will yield a calculated fat value of 1.9% for a carcass specific gravity of 1.105, which is the mean of the four highest specific gravity values above. The fat estimate of 1.9% appears reasonable for starved animals. Probably, the major contributing factor for the opossum's apparent higher lean density of 1.11 compared to published estimates is the additional high density contributed by the relatively large tail.

Results are presented in Tables 13, 14, 15 and 16, and in Figures 20, 21, 22 and 23. Winter body weight statistics and regression equations are given in Tables 13 and 14, and in Figures 20, 21 and 22. A total of 154 animals

Figure 20. Regression of body weight (Y) on days (X) of the winter period (December 1 = Day 1, March 29 = Day 120), of 138 opossums collected January through March, 1968, in southern Michigan. Four, rather than five 15-day weight classes have been used to calculate regression equations because of the lack of representation of females in the February 21 class. The asterisk denotes significance of the regression coefficient at the 95% confidence level.



ADULTS (N = 46)
Ŷ = 4359·6 − 13·89* X
ALL ANIMALS (N = 138)
Ŷ = 3012·4 − 7·67* X
JUVENILES (N = 92)
Ŷ = 2461·5 − 5·93* X
BODY WEIGHT · GRAMS
4000
3500
3000
2500
2000
1500
DEC. 8
23
JAN.7
22
FEB.6
21
MAR.7
22
29
MIDPOINTS, 15 DAY CLASSES

Figure 21. Regression of body weight (Y) on days (X) of the winter period (December 1 = Day 1, March 29 = Day 120), of 106 male opossums collected January through March 1968, in southern Michigan. The regression is based on five 15-day weight classes. The asterisk denotes significance of the regression coefficient at the 95% confidence level.

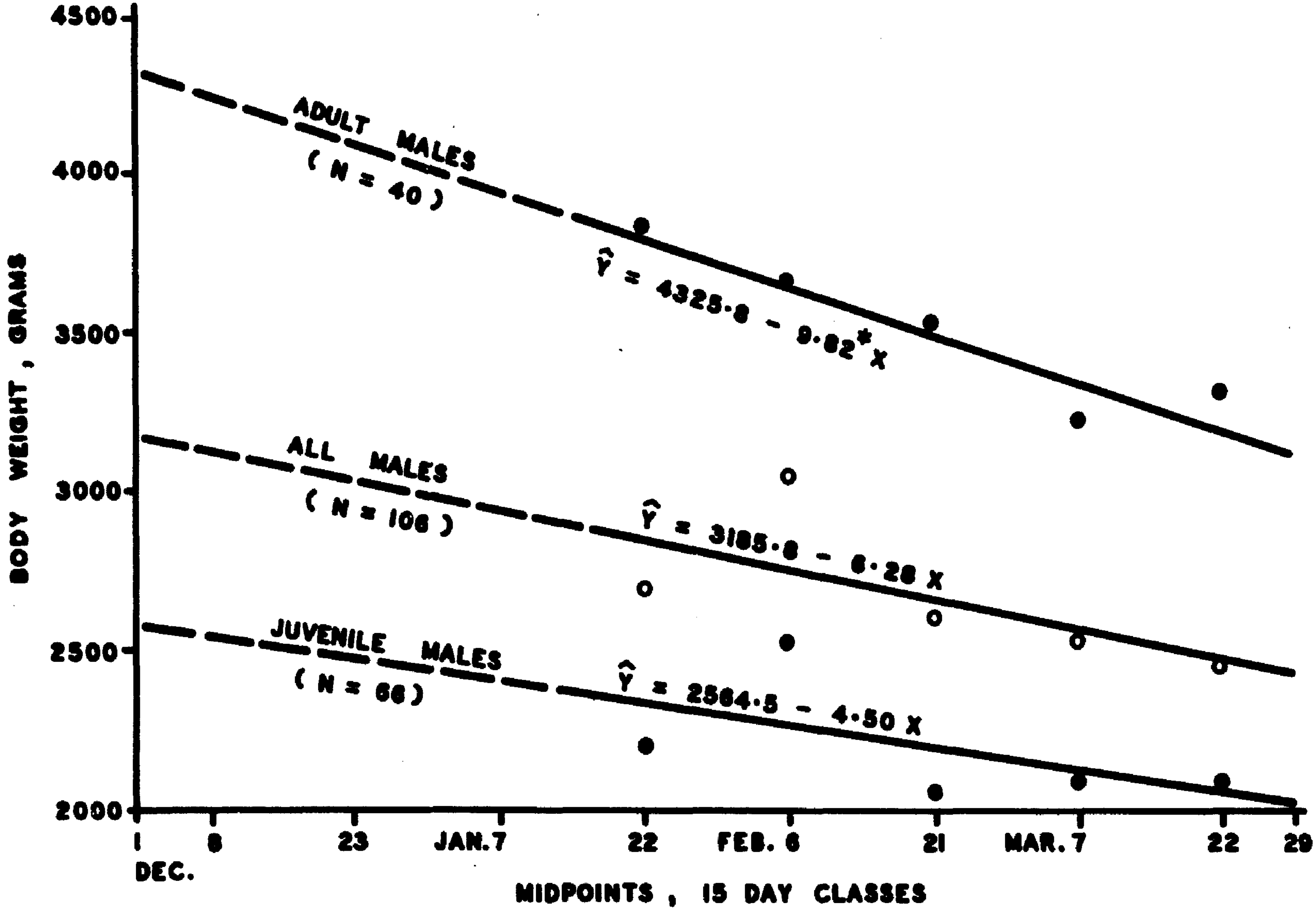

BODY WEIGHT , GRAMS
4500
4000
3500
3000
2500
2000
ADULT MALES
(N = 40)
$\hat{Y}$ = 4325·8 - 9·82* X
ALL MALES
(N = 106)
$\hat{Y}$ = 3185·8 - 6·28 X
JUVENILE MALES
(N = 66)
$\hat{Y}$ = 2564·5 - 4·50 X
1
DEC.
8
23
JAN.7
22
FEB. 6
21
MAR. 7
22
29
MIDPOINTS , 15 DAY CLASSES

Figure 22. Regression of body weight (Y) on days (X) of the winter period (December = Day 1, March 29 = Day 120), of 48 female opossums collected January through March, 1968, in southern Michigan. The regression is based on four, rather than five 15-day weight classes because of the lack of representation of females in the February 21 class. The asterisk denotes significance of the regression coefficient at the 95% confidence level.

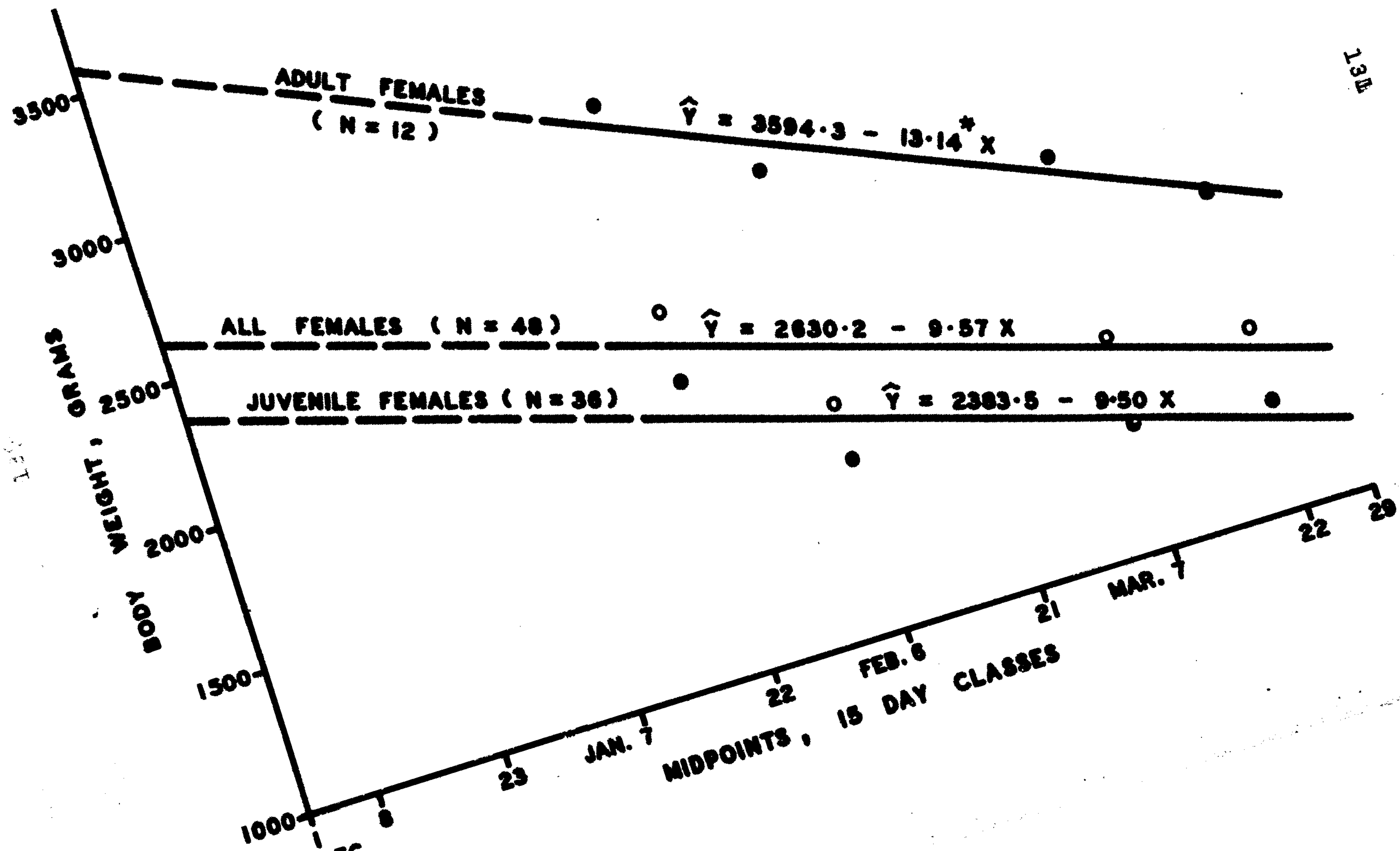

ADULT FEMALES
(N = 12)
Ŷ = 3594·3 − 13·14* X
ALL FEMALES (N = 48)
Ŷ = 2630·2 − 9·57 X
JUVENILE FEMALES (N = 36)
Ŷ = 2383·5 − 9·50 X
BODY WEIGHT, GRAMS
3500
3000
2500
2000
1500
1000
1 DEC.
8
23
JAN. 7
22
FEB. 6
21
MAR. 7
22
29
MIDPOINTS, 15 DAY CLASSES

Figure 23. Regression of the lipid fraction (%) of body weight (Y) on days (X) of the winter period (December 1 = Day 1, March 29 = Day 120) of 54 opossums collected from January through March, 1968, in southern Michigan. See text for determination of "heavy" and "light" animals.

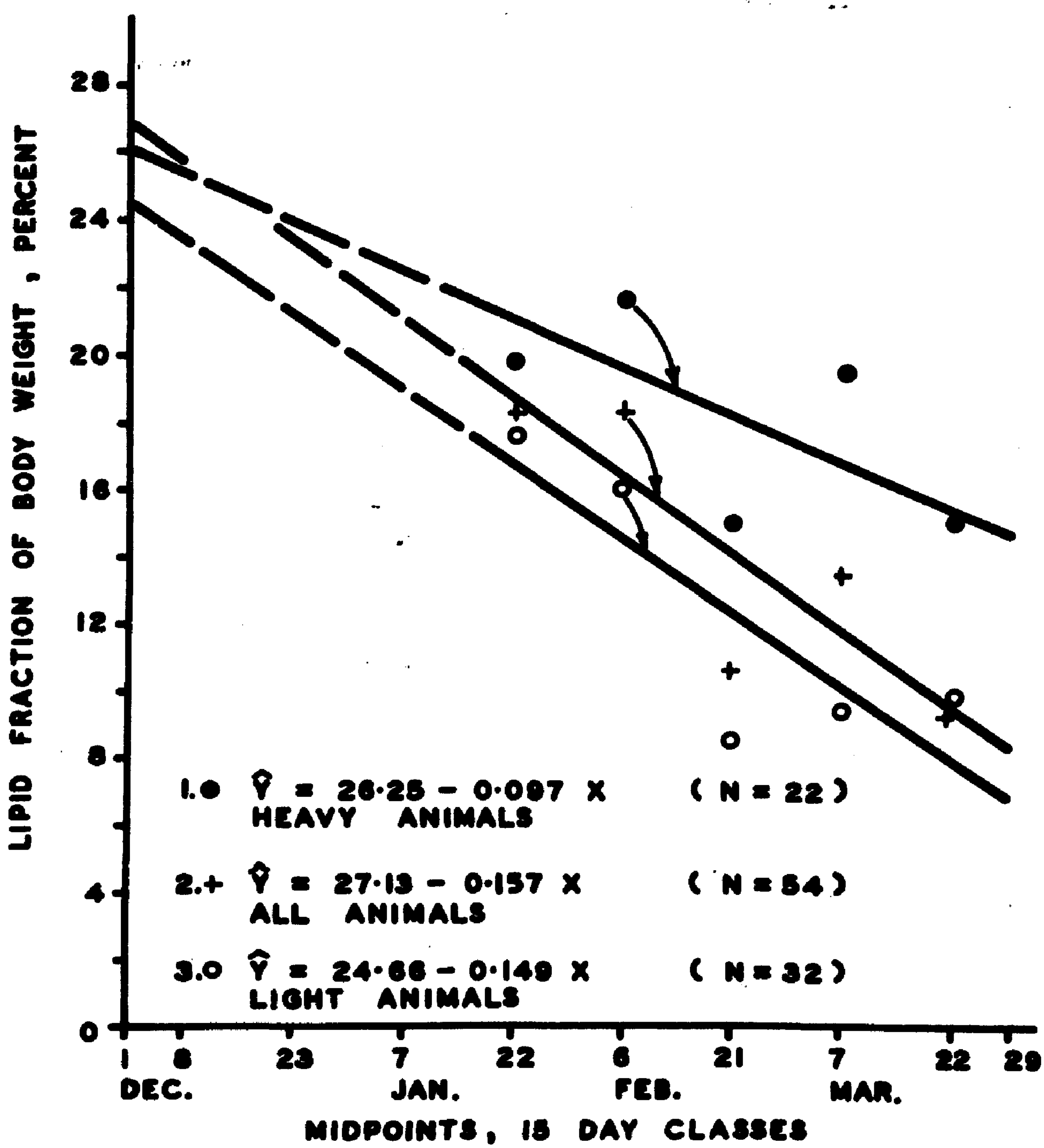

LIPID FRACTION OF BODY WEIGHT , PERCENT
0
4
8
12
16
20
24
28
1.● $\hat{Y}$ = 26·25 – 0·097 X (N = 22)
HEAVY ANIMALS
2.+ $\hat{Y}$ = 27·13 – 0·157 X (N = 54)
ALL ANIMALS
3.○ $\hat{Y}$ = 24·66 – 0·149 X (N = 32)
LIGHT ANIMALS
1
8
23
7
22
6
21
7
22
29
DEC.
JAN.
FEB.
MAR.
MIDPOINTS, 15 DAY CLASSES

Table 13. Body weight statistics of opossums collected January through March, 1968, in southern Michigan.

Description	Sample Size n	Mean Body Weight (g)	S.D. (g)	Range(g)
Males				
Adults	40	3556.5	456.7	2780 - 4620
Juveniles	66	2230.7	547.8	770 - 3290
Adults and Juveniles	106	2731.0	824.6	770 - 4620
Females				
Adults	12	2350.0	429.7	2040 - 3240
Juveniles	36	1628.6	456.8	710 - 3140
Adults and Juveniles	48	1808.9	550.6	710 - 3240
Males and Females				
Adults	52	3278.1	620.9	2040 - 4620
Juveniles	102	2018.2	590.8	710 - 3290
Adults and Juveniles	154	2443.6	859.7	710 - 4620

Table 14. Regression of body weight (g) on days of the winter period (Dec. 1 = Day 1; Mar. 29 = Day 120) of opossums collected January through March, 1968 in southern Michigan.

Description	Sample Size n	Regression Equation[1]	Values Calculated from the Regression Equation: Body wt.(g) Dec. 1 or Day 1	Body wt.(g) Day 60	Body wt.(g) Mar. 29 or Day 120	%wt. loss / 120 days
Males						
Adults	40	$\hat{Y} = 4325.8 - 9.82^{*}X$	4316	3727	3137	27.3
Juveniles	66	$\hat{Y} = 2564.5 - 4.50\ X$	2560	2294	2024	20.9
Adults and Juveniles	106	$\hat{Y} = 3185.8 - 6.28\ X$	3179	2809	2432	23.5
Females						
Adults	12	$\hat{Y} = 3594.3 - 13.14^{*}X$	3581	2806	2017	43.7
Juveniles	36	$\hat{Y} = 2383.5 - 9.50\ X$	2374	1813	1243	47.6
Adults and Juveniles	48	$\hat{Y} = 2630.2 - 9.57\ X$	2621	2056	1482	43.4
Males and Females						
Adults	46	$\hat{Y} = 4359.6 - 13.89^{*}X$	4346	3526	2693	38.0
Juveniles	92	$\hat{Y} = 2461.5 - 5.93^{*}X$	2456	2106	1750	28.7
Adults and Juveniles	138	$\hat{Y} = 3012.4 - 7.67^{*}X$	3005	2552	2092	30.4

[1] Y = body weight (g)
X = days of winter period

* t test of the regression coefficient significant at 95% level of confidence.

were processed, of which 68.8% (106) were males (Table 13) and 31.2% (48) were females (a ratio of 2.21 : 1.0), and 66.2% (102) were juveniles and 33.8% (52) were adults (ratio of 1.96 : 1.0). Juveniles are defined here as animals less than one year old. The higher sex ratio in favor of males may represent an actual preponderance of males, or a greater cruising radius for males, or both. The latter appears most likely. Sandidge (1953) reported that 53.9% of 560 opossums in Kansas (of which 426 specimens were pelts), were males; 58% of Hamilton's (1958) New York specimens were males. Fitch and Sandidge (1953) report a 1 : 1 sex ratio for 117 trapped specimens in Kansas.

The greater fraction of juveniles in the sample, approximately in the ratio of 2 : 1, is probably fairly representative of the population as a whole. Possibly the actual fraction of juveniles is higher because young individuals I have observed in the field have a smaller cruising radius than adults. Fitch and Sandidge (1953) found that the juvenile fraction ranged from 60.8% to 75% in three years of study in Kansas.

The data in Table 14 and Figure 20 indicate that the percent weight loss for adults (27.3%) exceeds that for juveniles (20.9%). I believe that this indicated relationship is erroneous - actually, the smallest juveniles apparently die before winter's end and hence the lightest cohorts are not represented in late winter samples. Thus, the weight loss of juveniles tends to be minimized. In this connection, the five smallest individuals were collected between January 19 and February 16. No specimens of this small size appeared in the collection after February 16. The body fat determinations of three of these small animals are as follows:

January 21, 1074 g weight, 8.5% body fat

January 31, 774 g weight, .5% body fat

February 6, 710 g weight, 11.8% body fat

These fat percentages are below the level required for winter survival, judging from the comparative value of 17.7% (Table 16) for mid-winter for all opossums analyzed. Also, the high significance (95% level) for the regression of juvenile weight is misleading because in individual male and female regressions, the considerable deviations of class means for January 22 and February 6 are complementary (Figures 21 and 22), resulting in significance for the pooled juvenile regression.

It appears that in general, the percent weight loss of females (Table 14, Figures 21 and 22) calculated from the regression equation is greater than that of males. This is to be expected since the calculated mid-winter mean weight of females is 753 g (Table 14) less than males, indicating highe metabolic requirements due to smaller size. It is of considerable interest that the percent weight loss for females appears to exceed the 40% level (Table 14). Judging from observations on penned animals, this is at, or near the limit of weight loss that can be sustained. Maximum recorded weight loss of penned animals was as follows: No. 1, 44.7%; No. 3, 42.5%; No. 4, 41.5%; No. 5, 39.5% (this animal almost died); No. 7, 42% (this animal died of starvation).

Following are data reported by other investigators on the winter weight loss of opossums and other mammals. Hamilton (1958) in New York recorded the weights of 38 different individuals in the months of December through March. Weights in March were 31% lighter for males and 38% lighter for females. Fitch and Sandidge (1953) in Kansas recorded the weights of the same individuals, trapped in the wild, October through March. An approximated mean weight loss (five individuals, interpreted from graph) for this period was 39%. One adult male, recaptured several times, had weights as follows: November 28, 1950, 4.54 kg; December 23, 5.00 kg; March 6, 3.08 kg; June 18, 2.62 kg. This animal lost 48% of its December weight in six months. In comparison, Michigan raccoons show a winter weight loss of 25% for females and 30% for males (computed from the data of Stuewer, 1943). Hibernating ground squirrels lose about 30% of their weight (Kayser 1962). Bailey and Davis (1965) report that the average woodchuck loses about 39% of its mean prehibernation weight. These data suggest that the opossum may lose a large fraction of its weight in winter, apparently larger than many other mammals.

Table 15. The lipid fraction of body weight of opossums collected January through March, 1968, in southern Michigan.

Description	Sample Size n	Mean Body Weight (g)	Range of Body Weights (g)	Lipid Fraction of Body Weight (%)	Range of the Lipid Fraction of Body Weights (%)
Males					
Adults	11	3548	2980 - 4170	17.6	5.3 - 25.4
Juveniles	23	2111	770 - 3090	13.7	0.0 - 28.2
Adults and Juveniles	34	2576	770 - 4170	14.9	0.0 - 28.2
Females					
Adults	7	2551	2040 - 3240	20.6	6.2 - 31.0
Juveniles	13	1492	710 - 2040	12.8	3.2 - 22.0
Adults and Juveniles	20	1863	710 - 3240	15.6	3.2 - 31.0
Males and Females					
Adults	18	3160	2040 - 4170	18.8	5.3 - 31.0
Juveniles	36	1888	710 - 3090	13.4	0.0 - 28.2
Adults and Juveniles	54	2312	710 - 4170	15.2	0.0 - 31.0

Table 16. Regression of the lipid fraction (%) of body weight on days of the winter period (Dec. 1 = Day 1; Mar. 29 = Day 120) of opossums collected from January through March, 1968, in southern Michigan.

Descripton	Sample Size n	Regression Equation[2]	Values Calculated from the Regression Equation: % Lipid Begin Winter Day 1	% Lipid Middle Winter Day 60	% Lipid End Winter Day 120	% Decline in Initial Lipid Fraction for 120 Day Winter Period
Heavy opossums[1]	22	$\hat{Y} = 26.25 - .097\ X$	26.1	20.4	14.6	44.1
Light opossums[1]	32	$\hat{Y} = 24.66 - .149\ X$	24.5	15.7	6.8	72.3
All opossums	54	$\hat{Y} = 27.13 - 1.57\ X$	27.0	17.7	8.3	69.3

[1] To divide "heavy" from "light" animals, the regression equation $Y = 3012.4 - 7.67\ X$ (Y = wt. in g, X = days of winter period) for all 154 animals for which weight was determined, was used. "Heavy animals" were above the line, "light" ones were below it.

[2] Y = Lipid fraction of body weight in %.
X = days of the winter period.

Statistics and regressions for winter decline in body fat are given in Tables 15 and 16 and Figure 23. The total sample size analyzed for body lipid content was 54 individuals, a number too small to be subdivided into age and sex groups for calculating regressions. Rather, lipid regressions were calculated for two sub-groups with weights falling above the weight regression for all animals (Table 14; Y = 3012.4 - 7.67 X*) - the "heavy opossums", and those falling below the regression - the "light opossums". These results are given in Table 16 and Figure 23. The regressions for percent fat are significant at the 10% level.

The mean lipid fraction of 18.8% (Table 15) for adult animals is higher than the corresponding value of 13.4% for juveniles. This is to be expected as the mean body weight of juveniles is 1.27 kg less than adults and hence have a higher metabolic rate per unit body weight. Likewise, the percent decline of body fat in light animals (Table 16) is greater than heavy animals by 28.2%.

The fat lost per unit body weight lost can be calculated from the lipid regression equation for all animals analyzed (Table 16), and their body weight regression (Y = 2853.4 - 6.9X* where Y = weight and X = days). This value is 0.73 g fat lost/g body weight lost. Thus, using a combustion value of 9.5 kcal/g fat, the energy provided by weight loss would be 6.9 kcal/g weight lost. For heavy animals, the equivalent value is 0.53 g fat/g body weight lost (using the regression for weight of Y = 3986.1 - 10.1X*, and the corresponding equation for lipid loss in Table 16. At 9.5 kcal/g fat, 1.0 g body weight supplies 5.03 kcal, which does not differ greatly from 4.4 kcal/g weight loss calculated by food balance for experimental animals.

CHAPTER X

ECOLOGICAL SYNTHESIS: MODELS OF WINTER ENERGETICS AND SURVIVAL

Several important features regarding the opossum's winter energy economy emerge from the data and observations presented in previous chapters. These are:

1. Labile thermoregulation and low body temperatures contribute to a low resting metabolic rate, among the lowest for non-hibernating mammals. Consequently, energy expenditure of sleeping opossums is low.
2. Denning behavior and the thermal characteristics of the ground burrow are such that the opossum's resting metabolic rate does not exceed the basal metabolic level of well-insulated species.
3. A great proportion of time is spent in winter sleep, suggesting considerable energy savings.
4. Depot fat appears to play a major role as an energy reserve. However, the fat depot supplies only enough energy for a maximum survival length approximately one-half of the winter period (unlike a true hibernator such as the woodchuck).

5. Generally, foraging is restricted to nights with temperatures around $0^{o}C$ or above.

   Foraging is also restricted by deep snow.

It is a fact that the opossum survives the temperate winter and is eminently successful alongside its specialized and well insulated competitors. The data and observations presented here suggest that the opossum compensates for its lack of predatory agility and inferior insulation by means of behavioral thermoregulation and low energy requirements. However, the opossum appears to have an ecological Achilles Heel in the form of two major limiting factors; (1) its physiological inability to forage at sub-freezing temperatures, and (2) the limitations imposed on foraging by deep snow. Both an excess of winter days with sub-freezing temperatures and deep snow would tend to limit energy intake. Both factors are a function of locality and latitude and in Michigan they tend to increase with increasing latitude. The objective of the mathematical models which follow is to quantify the limitations imposed by these factors on the opossum's winter energy budget and hence on its survival and distribution.

Let us assume that a hypothetical winter period of X days consists of various combinations of days spent in sleep (days when the maximum temperature does not exceed $0^{o}C$) and days on which animals forage (days when the maximum temperature exceeds $0^{o}C$). An energy parameter most critical to the opossum's winter energy balance is the minimum mandatory energy intake on those days available for foraging. This energy deficit per foraging day would tend to increase as fewer days for foraging are available in the winter period. The energy deficit per foraging day may be calculated for various winter combinations of sleeping and foraging days using a "representative opossum" of mean weight and characteristics. We may formulate as follows:

Key to symbols:

D_F = Foraging days in the winter period

D_S = Sleeping days in the winter period

D_L = Foraging days with complete lack of foraging success (ie., no energy intake)

E_S = Rate of energy expenditure per sleeping day

E_F = Rate of energy expenditure per foraging day

E_W = Energy provided per unit body weight lost

E_T = Total winter energy expenditure

E_{TF}= Total energy to be provided by foraging

E_D = Energy deficit/foraging day

(All energy values are kcal of metabolizable energy)

W = Maximum weight loss

K = Constant

Assuming that $D_S + D_F = K$

and total energy expenditure (E_T) for any given combination of foraging and sleeping days is

(1) $E_T = D_S E_S + D_F E_F$

and the total energy provided by maximum weight loss is

$$W E_W$$

and the total energy which has to be provided by foraging (E_{TF}) is

(2) $E_{TF} = D_S E_S + D_F E_F - W E_W$.

It follows that the energy deficit (E_D) per foraging day is given by the equation

(3) $$E_D = \frac{D_S E_S + D_F E_F - W E_W}{D_F} = \frac{E_{TF}}{D_F}$$

E_D can be calculated for various combinations of sleeping days and foraging days in the winter period. However, E_D is a theoretical value which does not allow for a lack of foraging success and it is a safe assumption that the opossum is not 100% successful on all foraging days. Calculation of all possible combinations of foraging success and failure is impractical as the number of possibilities is almost infinite. However, assuming complete failure for selected numbers of foraging days, the effect of lack of foraging success for various winter conditions is given by

(4) $$E_D = \frac{D_S E_S + D_F E_F - W E_W}{D_F - D_L} = \frac{E_{TF}}{D_F - D_L}$$

Using these relationships, three models of winter energy deficit and lack of foraging success have been calculated for representative opossums. These are:

<u>Model 1</u>, representing energy relations for all opossums.

<u>Model 2</u>, representing energy relations for adults only.

<u>Model 3</u>, representing energy relations for juveniles only.

Assumptions for Model 1 are given below. Assumptions for Models 2 and 3, derived in a similar manner, are given in Appendix A, pages 187 and 188.

<u>Assumptions for Model 1</u>

1. The critical winter period encompasses the months December through March (120 days), the period of greatest climatic severity in Michigan. This is also the usual period of greatest body weight decline for opossums. Peak weights for the year are reported to occur in November (Fitch and Sandidge, 1953) in Kansas and November and December (Hamilton 1958) in New York. Minimum annual weights occur in March and early April as indicated by data presented here and by Fitch and Sandidge (1953) in Kansas and Hamilton (1958) in New York. In terms of symbols used previously,

$$D_S + D_F = 120.$$

2. Animals sleep in the den on days when the maximum temperature does not exceed 0°C. All other days are potential foraging days. Although most activity ceases below 0°C (Chapter III), it was noted that activity for some animals was recorded at temperatures as low as -5°C. The point of division of 0°C rather than -5°C has been chosen here because on days with a maximum temperature of 0°C (at Lansing, Michigan) the mean air temperature has declined to about -4°C by 7:00 p.m. when animals became active and such days actually include a mean nightly minimum of -8.2°C (30 year mean, U. S. Weather Bureau).
3. The mean mid-winter body weight (Day 60) for males (2809g) and females (2056g) is 2.40 kg (rounded off from 2.43 kg), based on the weight regression equations (Table 14, Chapter IX) for all males (n = 106) and females (n = 48).
4. The maximum tolerable weight loss is 42% (Table 14, Chapter IX). Assuming a body weight of 2.40 kg at mid-winter, the body weight at the beginning of winter is 3.04 kg, and 1.76 kg at winter's end (at 42% weight loss). Thus the total body weight loss (W) during the winter is 1280 g and assuming that the metabolizable energy value (E_W) per unit weight lost is 4.4 kcal/g (Table 11, Chapter VIII, mean of all animals), the total energy provided by weight loss is 5632 kcal.

Assume $W\ E_W = 5630$ kcal.

5. The metabolizable energy expended per day while the animal (2.40 kg) is confined to the den is 113 kcal, based on a rate of 1.96 kcal/kg/hr (n = 7, Table 9, Chapter VIII).

Assume E_S = 113 kcal/day.

6. The metabolizable energy expended per foraging day is 158 kcal, based on a rate of 2.75 kcal/kg/hr (Table 10, Chapter VIII. The two lightest animals have been excluded from this rate calculation so that the mean M.E. of 6 animals weighing 2,38 kg is 2.75 kcal/kg/hr).

Assume E_F = 158 kcal/day.

7. There is obviously a limit to the amount of energy which can be ingested by an opossum in one foraging day. Conservatively, it may be assumed that the daily ingestion limit is the ultimate energy deficit per day which can be satisfied for any combination of winter conditions. The mean daily intake of rabbit flesh by experimental opossums feeding ad libitum was 120 g/kg body weight (Table 8, Chapter VIII). Assuming that the combustion value of whole cottontail rabbit is equal to that of Microtus, or 1.37 kcal/g wet weight (Golley 1960), and an efficiency of conversion to M.E. of 80% (Table 7, Chapter VIII), then the 288 g of rabbit ingested by a 2.40 kg opossum will have a M.E. value of 315 kcal. We may assume that 315 kcal is the maximum energy intake per foraging day.

Sample Calculation - Species Winter Energy Expenditure at Battle Creek, Michigan

At Battle Creek, there are 50 days (30 year mean, U.S. Weather Bureau) within the 120 day winter period with a maximum temperature of 0°C or below. These are winter sleep days. Potential foraging days are 120 - 50 = 70 days.

Given: D_S = 50 days

D_F = 70 days

D_L = 15 days

E_S = 113 kcal/day

E_F = 158 kcal/day

$W\ E_W$ = 5630 kcal

Total winter energy expenditure (E_T) for a 2.40 kg opossum (theoretical species mean) is

(1) $E_T = D_S\ E_S + D_F\ E_F$

$E_T = (50 \times 113) + (70 \times 158)$

$E_T = \underline{\underline{16{,}710 \text{ kcal}}}$

Total winter energy to be provided by foraging (E_{TF}) is

(2) $E_{TF} = D_S\ E_S + D_F\ E_F - W\ E_W$

$E_{TF} = 16{,}710 - 3630$ kcal

$E_{TF} = \underline{\underline{11{,}080 \text{ kcal}}}$

Energy deficit per foraging day (E_D) is

$$E_D = \frac{D_S\ E_S + D_F\ E_F - W\ E_W}{D_F} \tag{3}$$

$$E_D = \frac{11,080}{70}$$

$$E_D = \underline{\underline{158.3 \text{ kcal/day}}}$$

Energy deficit per foraging day (E_D) with a complete lack of foraging success for 15 days (D_L; ie., no energy intake for 15 days of foraging) is

$$E_D = \frac{D_S\ E_S + D_F\ E_F - W\ E_W}{D_F - D_L} \tag{4}$$

$$E_D = \frac{11,080}{70 - 15}$$

$$E_D = \underline{\underline{201.4 \text{ kcal/day}}}$$

Results and Inferences

Energy relationships were calculated for Models 1, 2 and 3 on the basis of assumptions and equations given above and in the Appendix. These values are presented in Tables 17 and 18, and Figures 24 and 25.

Mean species energy relationships (Model 1) are visually represented in Figure 24. It will be noted that the energy deficit increases ever more sharply in relation to a decreasing number of foraging days, or an increasing number of days spent in sleep. Assuming that an opossum is capable of garnering the maximum of 315 kcal on every foraging day

Table 17. Total energy expenditure for the winter period (120 days) and energy deficit per foraging day for various combinations of foraging days and days spent in sleep; for Models 1, 2 and 3.

		Available foraging days in the winter period (120 days), and days spent in winter sleep, in parentheses.										
		120 (0)	110 (10)	100 (20)	90 (30)	80 (40)	70 (50)	60 (60)	50 (70)	40 (80)	30 (90)	20 (100)
Model 1 All Animals $\bar{x}$ = 2.40 kg	Total (kcal/ 120 days)	18,960	18,510	18,060	17,610	17,160	16,710	16,260	15,810	15,360	14,910	14,460
	Deficit (kcal/ foraging day)	111	117	124	133	144	158	177	204	243	309	441
Model 2 Adults $\bar{x}$ = 3.30 kg	Total (kcal/ 120 days)	21,840	21,290	20,740	20,190	19,640	19,090	18,540	17,990	17,440	16,890	16,340
	Deficit (kcal/ foraging day)	117	123	130	138	149	162	180	205	242	305	429
Model 3 Juveniles $\bar{x}$ = 2.05 kg	Total (kcal/ 120 days)	18,480	17,960	17,440	16,920	16,400	15,880	15,360	14,840	14,320	13,800	13,280
	Deficit (kcal/ foraging day)	114	120	126	135	145	158	176	201	238	300	424

Table 18. Effect of lack of foraging success on the energy deficit (kcal) per foraging day for various combinations of foraging days, and days spent in winter sleep (120 day winter period). Calculations are for the whole population (ie. adults and juveniles, Model 1)

Number of Days with Complete Lack of Foraging Success	Available foraging days in the winter period (120 days) and days spent in winter sleep in parentheses									
	120 (0)	110 (10)	100 (20)	90 (30)	80 (40)	70 (50)	60 (60)	50 (70)	40 (80)	30 (90)
0 (Complete success)	111	117	124	133	144	158	177	204	243	309
5	116	123	131	141	154	170	193	226	278	371
10	121	129	138	150	165	185	213	254	324	464
15	127	135	146	160	177	201	236	291	389	619
20	133	143	155	171	192	222	266	339	486	928
25	140	151	166	184	210	246	304	407	649	1860
30	148	161	177	200	231	277	354	509	973	9280

Figure 24. Model 1. Relationships of winter energy deficit per foraging day (ie., minimum mandatory energy intake per foraging day) to the number of available enforced sleeping days and foraging days in the 120 day winter period. Calculations are based on a theoretical opossum representing the species as a whole, with mean species characteristics. Solid curves indicate the effect of a complete lack of foraging success for given numbers of days, on the energy deficit per foraging day. The maximum energy deficit per foraging day which can be sustained (315 kcal) is represented by the horizontal dashed line. Projected intersections of the energy deficit curves (solid lines) with the maximum energy deficit line (horizontal dashed line) indicate the maximum number of enforced winter sleep days which can be survived (see text).

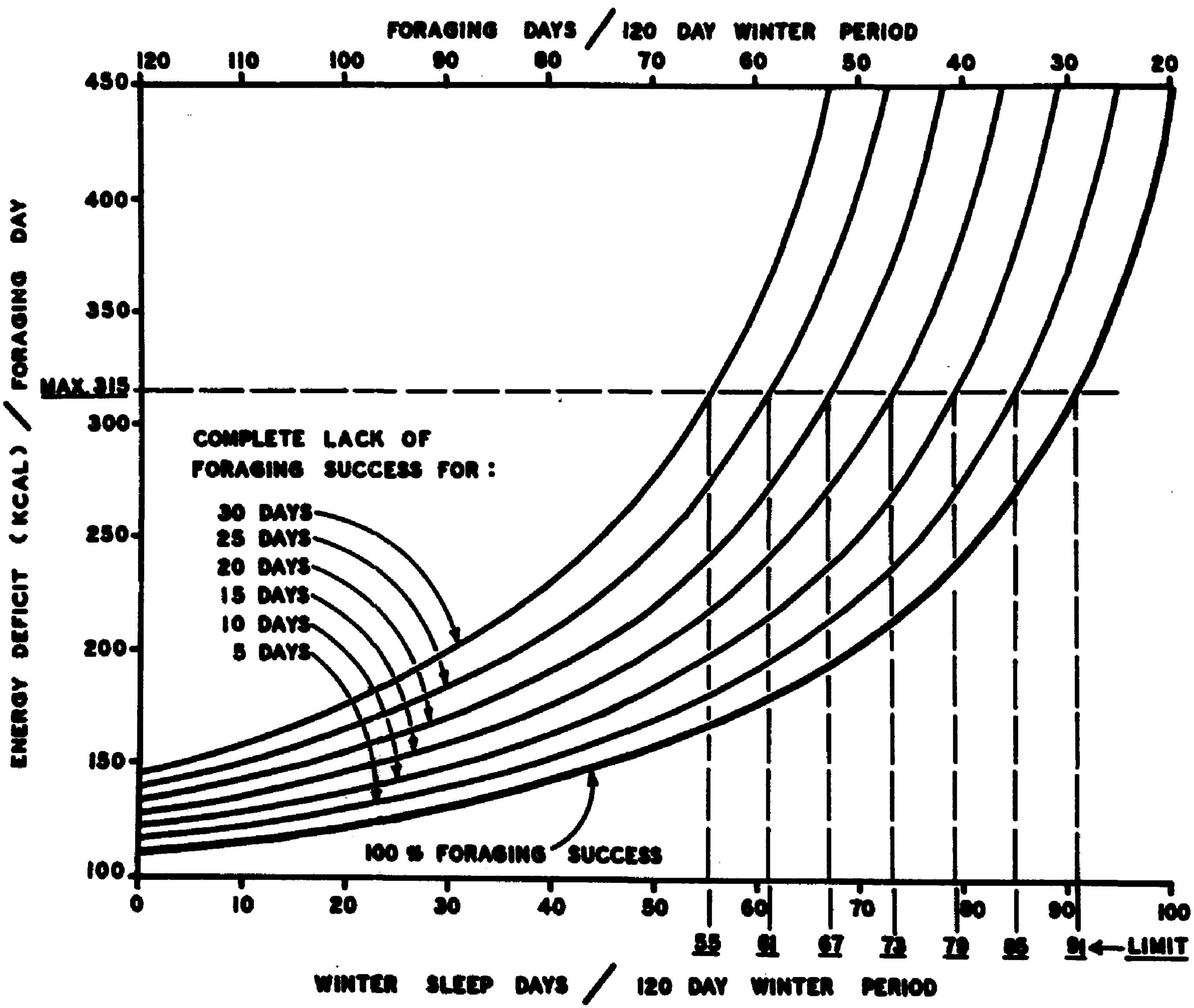
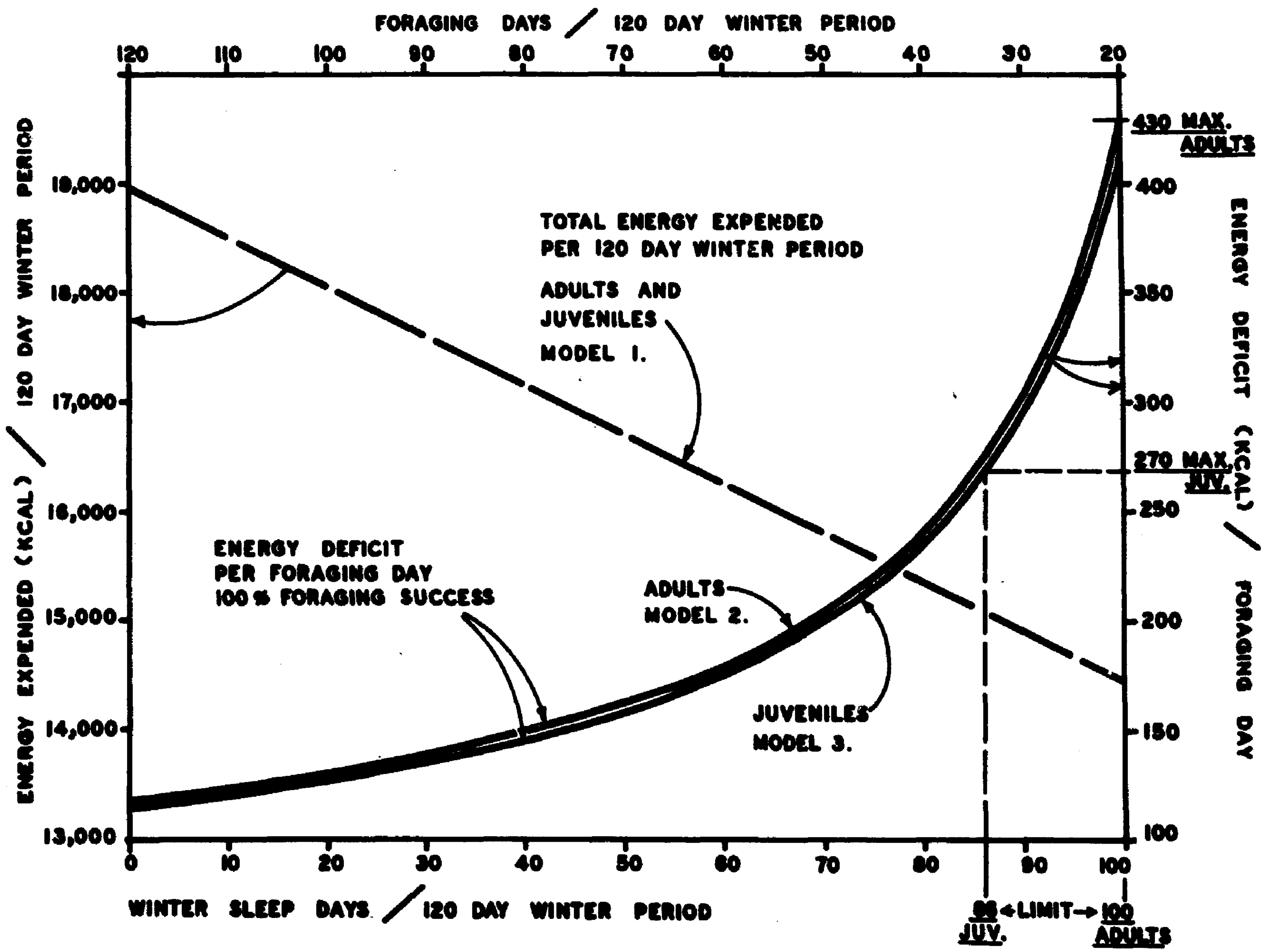

FORAGING DAYS / 120 DAY WINTER PERIOD
120 110 100 90 80 70 60 50 40 30 20
450 400 350 MAX. 315 300 250 200 150 100
ENERGY DEFICIT (KCAL) / FORAGING DAY
COMPLETE LACK OF FORAGING SUCCESS FOR:
30 DAYS
25 DAYS
20 DAYS
15 DAYS
10 DAYS
5 DAYS
100 % FORAGING SUCCESS
0 10 20 30 40 50 60 70 80 90 100
55 61 67 73 79 85 91 ← LIMIT
WINTER SLEEP DAYS / 120 DAY WINTER PERIOD

Figure 25. Model 2(Adults) and Model 3 (Juveniles). Relationships of winter energy deficit per foraging day (ie., minimum mandatory energy intake per foraging day) to the number of available enforced sleeping days and foraging days in the winter period (heavy solid curves). Calculations for each model are based on a theoretical opossum with mean characteristics of either adults (Model 2) or juveniles (Model 3) The maximum energy deficit per foraging day which can be sustained by adults and juveniles (430 and 270 kcal respectively) is represented by the horizontal dashed lines. Projected intersections of the two energy deficit curves (solid lines) with maximum energy deficit lines (horizontal dashed lines) indicate the maximum number of enforced winter sleep days which can be survived (see text). The broken, slanting line represents the total energy expenditure for the 120 day winter period for Model 1 in relation to the number of sleeping and foraging days.


FORAGING DAYS / 120 DAY WINTER PERIOD
120
110
100
90
80
70
60
50
40
30
20
ENERGY EXPENDED (KCAL) / 120 DAY WINTER PERIOD
19,000
18,000
17,000
16,000
15,000
14,000
13,000
TOTAL ENERGY EXPENDED
PER 120 DAY WINTER PERIOD
ADULTS AND
JUVENILES
MODEL 1.
ENERGY DEFICIT
PER FORAGING DAY
100% FORAGING SUCCESS
ADULTS
MODEL 2.
JUVENILES
MODEL 3.
430 MAX.
ADULTS
400
350
300
270 MAX.
JUV.
250
200
150
100
ENERGY DEFICIT (KCAL) / FORAGING DAY
0
10
20
30
40
50
60
70
80
90
100
WINTER SLEEP DAYS / 120 DAY WINTER PERIOD
86
JUV.
LIMIT
100
ADULTS

available, it could theoretically survive a winter with 91 enforced days of sleep and only 29 available foraging days. It is assumed, of course, that all body fat reserves are depleted. A lack of foraging success decreases the theoretical maximum number of enforced days spent in winter sleep (a function of winter severity) which can be survived (Figure 24). Each additional unit of five days of complete lack of foraging success will decrease by six the number of enforced winter sleep days which can be survived, or increase by six the number of necessary foraging days (Figure 24). No more than 55 enforced winter sleep days can be tolerated assuming a complete lack of foraging success for 30 days or some partial equivalent of the latter.

Energy deficit curves for Model 2 (adults) and Model 3 (juveniles) and total energy expenditure for Model 1 (mean species representative) are given in Figure 25. As might be expected, the total energy expenditure declines with increasing number of days spent in winter sleep. It is surprising that the energy deficit per foraging night is practically identical for juveniles and adults, (Table 17, Figure 25). There are two apparent reasons for this. Firstly, the greater individual mass of adults and consequently their greater energy expense, tends to be compensated by the higher metabolic rate of juveniles. It will be noted that the total energy expenditure of juveniles and adults (Table 17) differs only by a little over 3000 kcal for any combination of winter conditions. As I have observed previously (Chapter VIII), experimental opossums on a maintenance diet similarly had identical or nearly identical food requirements, regardless of body size. Secondly, the difference of approximately 3000 kcal of total energy expenditure between adults and juveniles is minimized farther by the additional 2950 kcal of energy in the fat depot of adults (7750 kcal) compared to juveniles (4800 kcal). Could it be that this equivalence of energy deficit is true for other wild species?

The near identical energy deficit per foraging day for juveniles and adults does not mean that their chances for winter survival are similar. The absolute theoretical limit of winter severity which can be survived is 86 days of enforced sleep for juveniles versus 100 days for adults (Figure 25). This theoretical difference is simply due to the greater daily intake capacity of adults compared to juveniles. One may also infer that the predatory success of adults is greater compared to that of juveniles. A large opossum (I have had them as large as 7.2 kg) can overpower most potential prey animals whereas a small opossum might conceivably fail to kill a rabbit as large or larger than itself. In the final analysis, long-term population survival depends on juvenile survival. The age ratio in the road-kill collection was 2 : 1 in favor of juveniles. It stands to reason that the winter energy relations of juveniles considered here are most relevant to population survival and species distribution.

CHAPTER XI

DISTRIBUTION

Elton (1927) wrote, "...Animals are in practice, limited in their distribution by their habits and reactions, the latter being so adjusted that they choose places to live which are suitable to their particular physiological requirements and their breeding habits." In previous chapters, I have attempted to show that energy limitations on the opossum's winter survival are a function of its physiology and ecology. In this section, data will be presented supporting the hypothesis that the northern distributional limit of the opossum is determined by the prevailing number of sub-freezing winter days and snow depth limiting winter energy intake, and hence limiting survival.

Theoretically and conservatively, energy limitations illustrated in Models 1, 2 and 3 (Chapter X) suggest that opossums cannot survive an excessive number of sub-freezing days (with enforced winter sleep), such that the energy deficit per foraging day exceeds the daily intake capacity of the individual. One may infer that the actual maximum limit of "winter severity" which can be survived is some lesser number of sub-freezing days and greater number of foraging days than the theoretical maximum. This appears to be the case, judging from distributional data. Distribution and relative density of opossums in Michigan are related to the number of sub-freezing winter days (enforced winter sleep days) in Figures 26 and 27. The opossum is rare to absent in areas with 70 or more winter days in which the maximum temperature does not exceed $0^{\circ}C$. (Note, the isotherms have been plotted on the basis of the annual number of days with daily maximum temperatures of $0^{\circ}C$ or below. About 90% of these days occur during December through March, the period used as a basis for calculations. Therefore, the approximate observed limits of tolerance as interpreted from the map in Figure 26 and 27 would be slightly lower than indicated). Conservatively, the observed limit of tolerance appears to be approximately 70 winter days with a maximum daily temperature of $0^{\circ}C$ or below, equivalent to 70 winter sleep days and 50 foraging days. The calculated total energy expenditure for 70 sleeping days and 50 foraging days for the "average opossum" (Model 1, Table 17 and Figure 24, Chapter X) is 15,810 kcal and the energy deficit per foraging day is 204 kcal, equivalent to approximately 18 days of complete foraging failure. It is interesting to note that the greatest density of opossums in southern Michigan (Taube 1942) appears to follow and occur south of the "50 day" isotherm (Figure 27).

Figure 26. Locations of road-killed opossums collected in Michigan from January through March, 1968, related to the number of days in winter with mean daily maximum temperatures equal to or less than $0^{\circ}C$ (numbers and heavy solid lines). Collecting effort was distributed throughout the state (collecting was done by the Michigan Department of Natural Resources). Climatalogical data are from the Weather Bureau, U. S. Department of Commerce.

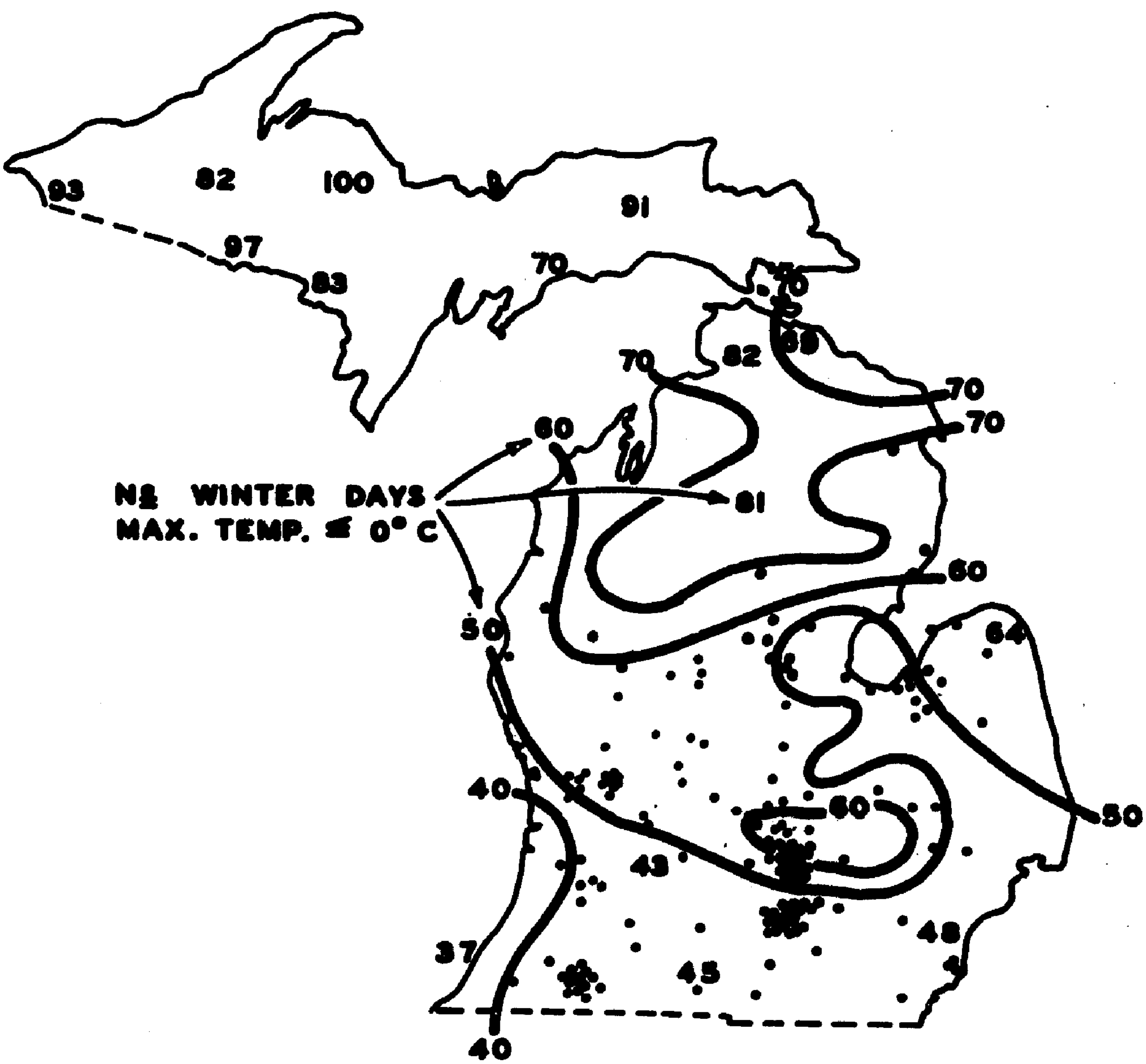
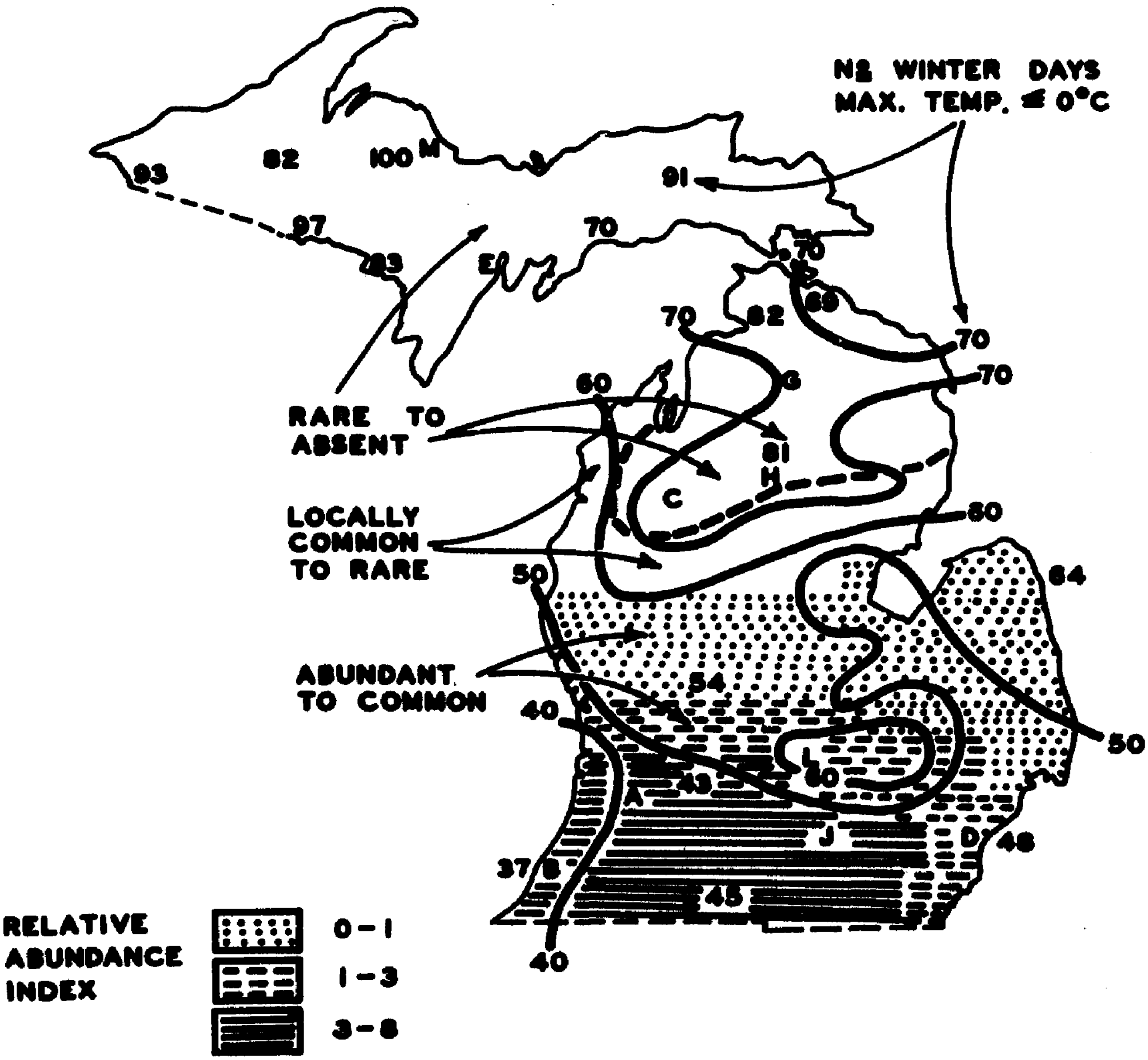

Nº WINTER DAYS
MAX. TEMP. ≤ 0° C
93
82
100
91
97
83
70
70
82
70
70
60
81
60
50
64
40
60
50
43
37
45
48
40

Figure 27. Opossum distribution and density in Michigan related to the number of days in winter with mean daily maximum temperatures equal to or less than 0°C (numbers and heavy solid lines). The relative abundance index represents opossums trapped per square mile from 1937 to 1941 (Taube, 1942). The heavy broken line represents the approximate northern distribution boundary, based on questionnaires. The letters represent cities, as follows: A Allegan, B Benton Harbor, C Cadillac, D Detroit, E Escanaba, G Gaylord, H Houghton Lake, J Jackson, L Lansing, M Marquette. Climatalogical data are from the Weather Bureau, U. S. Department of Commerce.

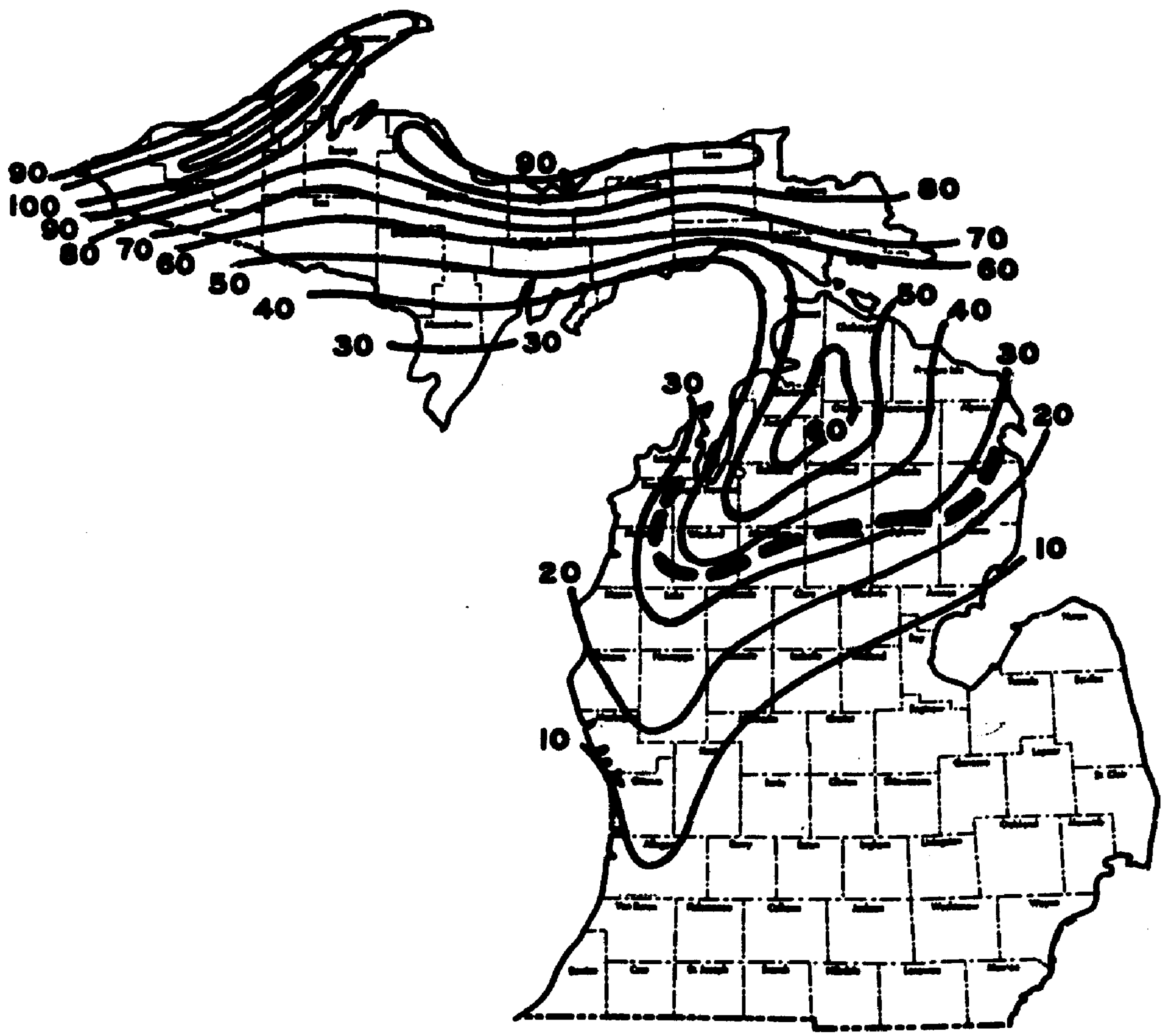


Nº WINTER DAYS
MAX. TEMP. ≤ 0°C
RARE TO ABSENT
LOCALLY COMMON TO RARE
ABUNDANT TO COMMON
93
82
100
M
91
97
83
E
70
70
69
70
82
70
70
60
G
81
H
C
80
50
64
54
40
43
L
60
A
J
D
48
37
B
45
40
50
RELATIVE ABUNDANCE INDEX
0–1
1–3
3–8

Comparison of distribution with winter snow in the state (Figure 28) shows that the observed limit of distribution also correlates approximately with snow depth. It is difficult to isolate the two climatic factors considered here. They complement each other in their negative effects and their combined negative effects increase northward. However, the apparent importance of snow depth is indicated by a population density comparison at the "60 day" isotherm near Lansing (Figures 27 and 28), and at the "60 day" isotherm farther north (Figures 26, 27 and 28). In the area of Lansing with relatively less snowfall, opossums are common. The population density drops off sharply at the more northerly locations where the mean number of winter days with accumulated snow depth on the ground of 28 cm or more exceeds 30 days (Figures 27 and 28).

Shelford (1911) noted, "The geographic range of any species is limited by the fluctuation of a single factor (or factors) beyond the limit tolerated by that species." In this vein, the main thesis proposed here is that "winter severity" is relevant to population survival only insofar as winter energy intake is limited by two factors: (1) the number of available foraging days is determined by the number of days in the winter period with maximum temperatures above $0^{\circ}C$, and (2) foraging success of the species is negatively affected by deep snow. If indeed these factors are important, it would follow that population declines are associated with

Figure 28. Mean number of winter days with accumulated snow depth on the ground of 28 cm or more. The heavy broken line represents the approximate northern distributional limit of the opossum. Snow map adapted from A. H. Eichmeier, 1964, Michigan Weather Service and Weather Bureau, U. S. Department of Commerce.


90
100
90
80
70
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severe winters. A well-documented population decline occurred in Allegan County, southwestern Michigan, following the severe winter of 1939 - 1940 (Stuewer, 1943). In 1939, 127 opossums were trapped in the wildlife refuge. In 1940, 24 opossums were trapped, with only five recaptures from the previous year. Allegan County has 41 days (mean) in December through March in which the maximum temperature does not exceed 0^{o}C. There were 12 fewer potential foraging days in the winter of 1939 - 1940 in Allegan County (interpreted from U. S. Weather Bureau records). Thus, 67 foraging days were theoretically available which is quite adequate under normal conditions of snow (Figure 27). Assuming a maximum energy intake of 315 kcal/foraging night (Model 1, Figure 24, Chapter X), more than 30 days with a complete lack of foraging success, or some partial equivalent of it, could have been sustained. Apparently, excessive snow depth adversely affected foraging to an equivalent of more than 30 days of complete foraging failure. Stuewer (1943) reports "two or more feet" of snow on the ground in January and March. Allegan County had a mean unmelted snowfall of 30 cm for the four winter months of 1939 - 1940 (U. S. Weather Bureau). The average snowfall for Michigan for 1940 was the greatest on record, amounting to 210 cm compared to the normal 143.2 cm. Metzger (1955) ascribes the decline of a local opossum population in Ohio to a severe winter. Peterson and Downing (1956) suspect that population fluctuations in southern Ontario have been caused by severe winters.

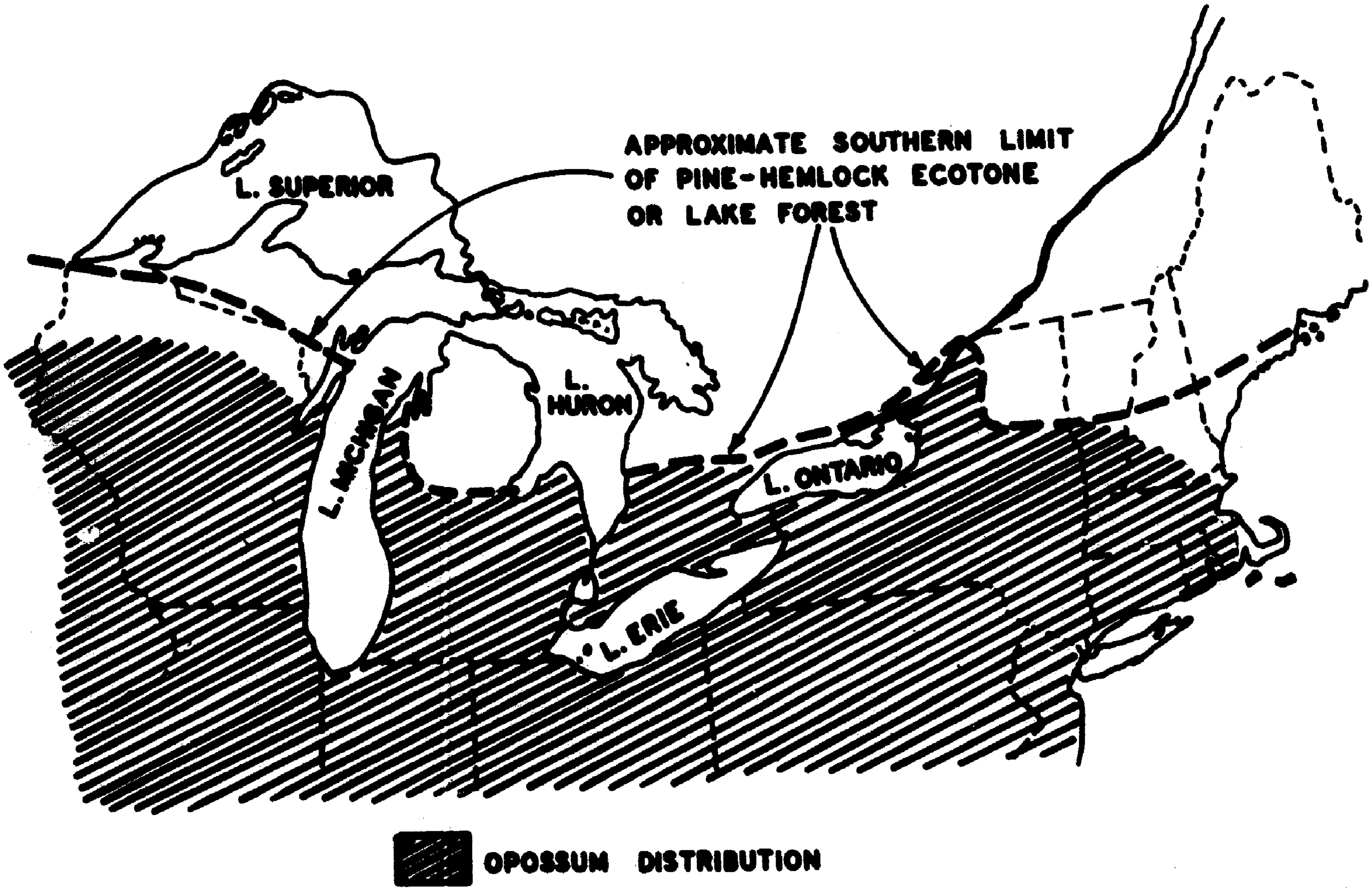
From my own observations, a significant population decline occurred at Kensington Park in south-eastern Michigan (a natural area) following the winter of 1961 - 1962. Apparently, both a lack of available foraging days and deep snow caused the decline. This winter had the lowest mean temperature since 1936, and the greatest snowfall (mean of 16 cm) in January, February and March since 1943. There were 67 days when the maximum temperature did not exceed freezing, five more days than the mean value. Taube (1942) reports declines in opossum trapping success in Michigan following "hard winters."

Of particular interest is an apparent population decline of major proportions which occurred around 1850 (Taube 1942). Early sighting records compiled by Taube show that this species occurred in the southern-most portion of Michigan from 1822 to 1850. He found no records of opossums occurring in the state between 1850 and 1897. An exceptionally severe winter was reported to have occurred around the middle of the century (cannot be verified by Weather Bureau). From data compiled by a Wisconsin conservation department official (Taube 1942), the opossum was scarce in Wisconsin during approximately the same period. A synchronous population decline of such wide magnitude implicates climatic factors.

The question arises whether there are any other important factors limiting northern distribution in Michigan. I believe this is quite unlikely. The opossum occupies an extremely diversified ecological niche, occurring in most terrestrial habitats within its range. Today, the opossum is found from the tropics north through the temperate region of eastern North America and has been locally successful in the West. Climatic factors are most likely to affect the distribution of a species with such non-specialized ecological requirements. This inference is supported by comparisons between ecologically similar areas in Michigan which differ greatly in degree of opossum abundance. For example, the oak forest association occurring on the sandy soils of Allegan County in southwestern Michigan (see city of Allegan, Figure 27) harbors a moderate opossum population. In the similar oak forests of Roscommon County (see Houghton Lake, Figure 27) and other similar areas to the north, the species is rare to absent. Opossums are common in the mixed hardwood forest, shrubland and alder thickets on the podzol soils of Gratiot County in the southern part of the state. They are absent from practically identical ecological associations occurring frequently in northern Michigan. Opossums are common in the beech-maple region of south-central Michigan (see Lansing, Figure 27). They are rare to absent from the beech-maple forests of Wexford County (see Cadillac, Figure 27). Another tempting (if improper) comparison; the raccoon occurs throughout the state (common in the Lower Peninsula, rare in the Upper Peninsula according to Stuewer 1943 and Burt 1954) compared to the absence of the opossum from roughly one-half of the state. Both animals are omnivorous and both spend much of the winter period in sleep.

The most sensitive indicators of climate are ecological. It is therefore useful to compare opossum distribution with regional vegetational and faunal associations. In Michigan, the present northern distributional limit of the opossum (Figure 29) coincides approximately with the southern edge of the pine-hemlock ecotonal region (or lake forest, which also includes yellow birch, sugar maple and beech as dominants) between the boreal coniferous forest region and the deciduous forest region (Nichols 1935, Shelford and Olsen 1935, Shelford 1963). This region has climatic, edaphic, vegetational and faunal affinities with the boreal coniferous forest. As a tentative hypothesis, I propose that the southern edge of the pine-hemlock ecotone approximates the northern potential distributional limit for the opossum in eastern North America. North of this boundary, winter energy availability is limited by the climatic factors which have been considered in this study and survival is therefore impossible. As of this writing, distributional data appear to support this hypothesis (Figure 29); in a general way, the distribution of the opossum has not extended north of this line. It is conceivable that local populations

Figure 29. The present approximate northern distributional limit of the opossum in the northeastern United States and adjacent Canada in relation to the southern edge of the pine-hemlock (lake forest) ecotone region (Nichols 1935, Shelford 1963). The northern distribution of the opossum is based on the following sources: Wisconsin, Jackson (1961), Long and Copes (1968); Michigan, present study; Ontario, Peterson and Downing (1956), Peterson (1966); New York, Hamilton (1958); Vermont, New Hampshire and Massachusetts, Waters and Rivard (1962).


APPROXIMATE SOUTHERN LIMIT
OF PINE-HEMLOCK ECOTONE
OR LAKE FOREST
L. SUPERIOR
L. MICHIGAN
L. HURON
L. ONTARIO
L. ERIE
OPOSSUM DISTRIBUTION

may become established to the north of the theoretical boundary wherever man has created an exceptional source of available energy, such as a garbage dump. However, it is doubtful that such marginal populations will long survive the vagaries of climate.

The validity of the latter hypothesis remains to be tested. For the Lower Peninsula of Michigan, there is good evidence that the opossum has marched as far north as it can go, as its range has not changed substantially for the last 25 years (Taube 1942 and present study). In Wisconsin, the opossum may extend its range northward (Figure 29). There have been recent records for northern Wisconsin (Long and Copes, 1968) and along the southern political boundary of Michigan's Upper Peninsula (Ozoga and Gaertner 1963, Rafferty, personal communication 1967). Perhaps the opossum will extend its range northward in the New England states. The ecotonal boundary has less predictive value there as the ecology of the region is far more complex than illustrated in Figure 29.

The northward spread of the opossum appears to be a phenomenon of historic times (Guilday 1958). Opossum remains are associated with archeological sites to the south of Michigan along the Ohio River and its tributary and Miami River, the southern shore of Lake Erie and south of the Hudson River valley along the Atlantic coast (Guilday 1958). Apparently it occurred at the edge of the prairie, south of Chicago (Liette, 1702). Early sightings of the opossum in Michigan (summarized by Taube 1942) followed the white man's pioneering activities. Corresponding northward population spread occurred throughout the East and Mid-west (Seton 1909, Goodwin 1935, Peterson and Downing 1956, Hamilton 1933, 1958, and others).

One may infer that agricultural practices and associated early seral stages provided favorable conditions for population expansion. In Michigan, the white man vastly increased (artificially) the prairie and forest edge habitats from the few, small, natural prairie remnants present in the original climax forest of the southwestern portion of the state (Veatch 1927). Pioneering caused a general increase in forest edge species (Seton 1909), such as the fox squirrel (Allen 1943) while the climax forest association declined. In the case of the opossum, this species is not a member of the forest-edge faunal association by virtue of any particular specialization or requirements. Man's pioneering activities may have caused population expansion by benefitting the species winter energy economy. Farm crops provide concentrated, easily available energy which may be important under survival conditions. Also, various foods are more available at ground level (where the opossum forages) in early seral stages than they are in the climax forest.

There is another possibility suggested by the findings of this study. Perhaps man has been the agent for the opossum's success by inducing an increase in the abundance and variety of burrowing mammals characteristic of the prairie and forest edge. It has been noted previously that the opossum is obliged to use the burrows of other mammals. Survival in the temperate winter depends on the ground microclimate, judging from the data presented. The increase in burrows may have provided minimal requirements for population expansion. Today, the principle terrestrial burrowing mammals in Michigan occurring throughout the state are the woodchuck, red fox, striped skunk and badger. Seton (1909) presents evidence that the red fox was not present in the primeval temperate deciduous forest. The striped skunk is an animal of the forest edge (Seton 1909 , Burt 1954) and apparently increased following settlement (Seton 1909). The badger frequents the prairie and forest edge (Seton 1909, Burt 1954) and probably also increased. Today, the badger is uncommon in Michigan, although it is distributed throughout the state. It does, however, leave a significant legacy in dens. Seton (1909) expresses the opinion that the woodchuck increased coincident with lumbering and farming. It is interesting to note that the opossum did occur along the edge of the prairie, south of Chicago before settlement began (Liette 1702). Other (typical) species present in the primeval forest climax community either did not produce ground dens (gray fox) or could hardly have produced a significant number of ground dens (gray wolf). One may infer that ground dens increased after settlement permitting population expansion of the opossum. If indeed this was the case, the opossum has invaded much of the temperate environment on the coattails of the burrowing mammals.

CHAPTER XII

CONCLUSIONS

By most measures, the didelphids are a successful group. They have survived with little morphological change for 70 million years or more (Simpson 1935) while many specialized marsupials and placentals have faded into extinction. With the re-establishment of the Pleistocene land bridge, the opossum was one of the few South American species which successfully invaded the domain of North American placentals. The opossum's success has been attributed to its structural generalization and non-specialized behavior. Its physiological-behavioral response to winter outlined here, appears to be but another facet of its generalized nature.

Winter survival for mammals is, in large measure, a problem of energy economy. Placental mammals have evolved mechanisms to cope with the temperate winter such as effective body insulation, huddling behavior, use of insulated shelters, food storage, hibernation and other means. From an energetics standpoint, the opossum's labile thermoregulation and low metabolic rate, coupled with its use of ground dens in winter is a notable and unusual response among mammals affecting winter energy economy. If the opossums physiological-behavioral response is as successful as it appears to be, why is it so poorly represented among northern mammals? I believe that the answer has ecological roots. The general trend in mammalian evolution has been one of specialization. Through specialization, utilization of energy in the ecosystem has been more efficient. It appears that the price for specialization has been a higher level of metabolism. Yet it seems that unexploited portions of many other niches do exist, particularly in the disturbed communities associated with man, which provide enough energy to sustain a species specializing in generalization. That species is the adaptable opossum. In short, perhaps the opossum's physiological-behavioral response to winter is a unique one because potential generalized niches to accommodate a low-key mode of life are restricted.

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APPENDICES

APPENDIX A

TABLES AND DERIVATIONS

APPENDIX A

TABLES AND DERIVATIONS

Table 19. Location description of ground dens. These dens were located in Area I.

Den No.	Location Description
1	Located in open, level grassland under a small cherry tree with a slight southern exposure; two entrances.
2	Located on an open, grassy ridge with scattered shrubs and a slight western exposure; two entrances.
5	A shady location under dense honeysuckle shrub growth in an immature stand of black locust with a slight western exposure; one entrance.
6	A relatively shady location in a black oak and beech forest; two entrances.
7	A relatively shady location on a forested knoll of oak, beech and elm with an eastern exposure; four entrances.
9	Located in open grassland under a hawthorn bush with a southern exposure; one entrance.
10	Located in a low lying aspen stand with a north-western exposure; one entrance.

Table 20. Opossum activity as a function of temperature in activity units/animal/hour. Figures in parentheses are the number of hours in which recorded activity fell into the corresponding temperature classes.

Periods	Temperature Classes							
	-20.0 to -15.1	-15 to -10.1	-10 to -5.1	-5 to -0.1	0 to 4.9	5.0 to 9.9	10 to 14.9	15 to 20
Fifteen day Periods								
Feb. 18 - Mar. 4 (120 opossum nights)	0(7)	.68(49)	1.54(65)	2.23(29)	-	-	-	-
Mar. 4 - Mar. 19 (105 opossum nights)	0(4)	.15(13)	1.46(22)	3.28(37)	4.16(45)	4.79(17)	3.08(2)	-
Mar. 19 - Apr. 3 (103 opossum nights)	-	-	0 (3)	2.41(48)	4.20(38)	6.47(31)	4.12(25)	-
Apr. 3 - Apr. 18 (117 opossum nights)	-	-	-	5.87(23)	6.38(40)	6.59(37)	7.97(35)	4.43(20)
Apr. 18 - May 3 (114 opossum nights)	-	-	-	2.93(13)	4.25(38)	5.79(50)	5.07(46)	5.14(3)
Total Period								
Feb. 18 - May 3 (75 nights, 559 opossum nights)	0(11)	.57(62)	1.47(90)	3.16(150)	4.74(161)	6.04(135)	5.75(108)	4.52(23)
Standard Deviation S		.47	1.05	1.66	1.70	1.77	3.46	1.52
Standard Error $S_{\bar{x}}$		.06	.11	.13	.13	.15	.33	.32

Table 21. Opossum activity as a function of time of night, in activity units/animal/hour. All activity values are hourly means.

	Hours of the Night P.M.										
	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
Feb. 18 - Mar. 4				.06	.09	.21	1.53	2.82	2.56	1.87	1.48
Mar. 4 - Mar. 19	.09	.23	.41	.41	.48	.68	1.94	3.48	3.84	3.52	4.27
Mar. 19 - Apr. 4		.05	.01	.08	.22	.42	1.16	3.07	3.59	4.01	4.19
Apr. 4 - Apr. 18					.02	.12	.30	3.23	5.38	5.79	7.09
Apr. 18 - May 3							.02	1.29	3.15	4.78	5.53
Mean - All Periods	.02	.05	.08	.10	.15	.27	.97	2.76	3.70	3.99	4.51

	Midnight		Hours of the Night A.M.							
	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9
Feb. 18 - Mar. 4	1.38	1.25	.92	.34	.29	.26	.13	.01		
Mar. 4 - Mar. 19	3.75	3.05	2.58	2.32	1.68	1.33	.92	.38	.07	
Mar. 19 - Apr. 4	4.45	4.27	4.78	4.48	4.15	3.17	2.42	1.28	.23	.13
Apr. 4 - Apr. 18	7.40	8.78	8.55	8.02	6.85	5.60	3.51	.61	.07	.04
Apr. 18 - May 3	5.95	6.10	5.99	5.62	4.93	4.27	1.83	.15		
Mean - All Periods	4.58	4.71	4.58	4.16	3.58	2.93	1.76	.47	.07	.03

Table 22. An example of data used to calculate the maintenance energy requirement for an opossum (No. 1). The period used to calculate maintenance energy for minimum activity was Feb. 24 to Mar. 3 when body weight remained essentially constant. Other periods used representing higher activity levels were Mar. 3 to 26, Mar. 9 to 17 and Mar. 9 to 26.

Date	Food Eaten (g)	Body Weight (g)	Activity Span (hours)	Total Activity Units	Mean Temp. (C°)
Feb. 24	115	1830	3	25	-8.6
25	0	-	0	0	-6.6
26	0	-	0	0	-3.3
27	0	-	2	6	-2.8
28	0	-	4	9	-5.5
29	0	1615	1	4	-9.2
Mar. 1	100	-	10	17	-4.7
2	0	-	2	4	-6.3
3	100	1814	3	9	-2.7
4	0	-	6	9	0.5
5	0	-	4	8	-1.9
6	0	-	-	-	-3.9
7	90	-	5	12	2.2
8	0	-	13	35	8.9
9	110	1758	18	48	5.0
10	0	-	7	17	-1.9
11	0	-	4	8	-1.1
12	0	-	7	15	-9.2
13	0	-	7	20	-7.9
14	140	1701	12	40	-0.5
15	0	-	8	21	4.4
16	0	-	7	63	4.4
17	110	1758	14	49	7.0
18	0	-	7	17	7.7
19	0	-	13	66	11.6
20	120	1729	8	23	4.4
21	0	-	4	20	0.0
22	0	-	7	15	-4.4
23	0	-	8	16	-4.2
24	140	1672	15	48	0.3
25	0	-	11	72	8.3
26	120	1814	8	20	10.0

FORMULA FOR THE CALCULATION OF PERCENT BODY FAT FROM DENSITY DETERMINATIONS

Specific gravity is given by the general formula:

$$\text{Specific Gravity} = \frac{\text{Weight of the Body}}{\text{Weight of an equal Volume of Water}}$$

or

$$\text{Specific Gravity} = \frac{\text{Weight of Body in Air}}{\text{Wt. of Body in Air} - \text{Wt. of Body in Water}}$$

On this basis, Kraybill et al. (1951, 1952) developed a formula for calculating the percent fat in an animal's body using density estimates for the fat and lean components of the carcass and determining the specific gravity of the whole animal. The derivation of this formula is given below.

Symbols:

W_B = Weight of body in air

W_F = Weight of fat in air

D_L = Density of lean component

D_F = Density of fat component

S_G = Specific gravity of the eviscerated carcass

$$\frac{W_F}{D_F} + \frac{W_B - W_F}{D_L} = \frac{W_B}{S_G}$$

$$\frac{W_F\ (D_L - D_F)}{D_F\ D_L} = \frac{W_B\ (D_L - S_G)}{S_G\ D_L}$$

$$\frac{W_F}{W_B} = \frac{D_F\ D_L - D_F\ S_G}{D_L\ S_G - D_F\ S_G}$$

$$\frac{W_F}{W_B} = \frac{D_F\ D_L}{S_G\ (D_L - D_F)} - \frac{S_G\ D_F}{S_G\ (D_L - D_F)}$$

Assume that D_F = .912, based on the work of Morales et al. (1945), for guinea pigs. This is similar to fat density values reported by other workers. Assume that D_L = 1.11. The latter value is based on the four lowest densities of whole (eviscerated) opossums as follows: 1.102 (animal died of starvation), 1.107, 1.108 and 1.102, with a mean value of 1.105. (The percent fat calculated for a body density value of 1.105 using D_L = 1.11 is 1.9%, a reasonable value for a starved animal).

Using D_F = .912 and D_L = 1.11, the general formula for opossums is derived as follows:

$$\frac{W_F}{W_B} = \frac{D_F\ D_L}{S_G\ (D_L - D_F)} - \frac{S_G\ D_F}{S_G\ (D_L - D_F)}$$

or

$$\%\ \text{Opossum Fat} = 100\left(\frac{.912 \times 1.11}{S_G\ (1.11 - .912)} - \frac{.912}{1.11 - .912}\right)$$

$$\%\ \text{Opossum Fat} = 100\left(\frac{5.111}{S_G} - 4.606\right)$$

Assumptions for Model 2 (Adults)

1. As in Chapter X.

2. As in Chapter X.

3. The mean mid-winter body weight (Day 60) for adult males (3727 g) and adult females (2806 g) is 3.30 kg (rounded off from 3.27 kg), based on weight regression equations in Table 14, Chapter IX for adult males (n = 40) and adult females (n = 12).

4. The maximum tolerable weight loss is 42% (Table 14, Chapter IX). Assuming a body weight of 3.30 kg at mid-winter, the body weight at the beginning of winter is 4.18 kg, and 2.42 kg at winter's end (at 42% weight loss). Thus the total body weight loss (W) during the winter is 1760 g, and assuming that the metabolizable energy value (E_W) per unit weight lost is 4.4 kcal/g (Table 11, Chapter VIII, mean of all animals), the total energy provided by weight loss is 7744 kcal.

   Assume W E_W = 7750 kcal

5. The metabolizable energy expended per day while the animal (3.30 kg) is confined to the den is 127 kcal. This value was selected as follows: The two largest opossums (No. 2 and 7, Chapter VIII, Table 9), have a mean winter weight of 2.99 kg and a mean M. E. expenditure (for minimum activity) of 1.68 kcal/kg/hr. As the mean weight of 2.99 kg of these two animals is less than the model mean of 3.30 kg, a lesser M. E. expenditure rate of 1.60 kcal/kg/hr compared to 1.68 kcal/kg/hr was arbitrarily selected for the larger theoretical mean weight of 3.30 kg, giving a daily rate of 127 kcal.

   Assume E_S = 127 kcal/day

6. The metabolizable energy expended per foraging day is 182 kcal, based on mean M. E. rate of 2.31 kcal/kg/hr for animals No. 2 and 7 (Table 10, Chapter VIII).

   Assume E_F = 182 kcal/day

7. The maximum M. E. intake is 131 kcal/kg body weight/day (Chapter VIII). For a 3.30 kg animal, the maximum M. E. intake is 432.3 kcal. Assume that the maximum M. E. intake per day is 430 kcal.

Assumptions for Model 3 (Juveniles)

1. As in Chapter X.

2. As in Chapter X.

3. The mean mid-winter body weight (Day 60) for juvenile males (2294 g) and juvenile females (1813 g) is 2.05 kg, based on weight regression equations in Table 14, Chapter IX for juvenile males (n = 66) and juvenile females (n = 36).

4. The maximum tolerable weight loss is 42% (Table 14, Chapter IX). Assuming a body weight of 2.05 kg at mid-winter, the body weight at the beginning of winter is 2.59 kg, and 1.50 kg at winter's end (at 42% weight loss). Thus, the total body weight loss (W) during the winter is 1090 g and assuming that the M.E. value (E_W) per unit weight lost is 4.4 kcal/g (Table 11, Chapter VIII, mean of all animals), the total energy provided by weight loss is 4796 kcal.

   Assume $W\ E_W$ = 4800 kcal.

5. The M.E. expended per day while the animal (2.05 kg) is confined to the den is 102 kcal/day, based on the M.E. rate of 2.07 kcal/kg/hr of animals No. 1, 3, 4, 5 and 6 for minimum activity (Table 9, Chapter VIII; the latter animals had a mean weight of 2.14 kg).

   Assume E_S = 102 kcal/day

6. The M.E. expended per foraging day is 154 kcal, based on a mean M.E. rate of 3.14 kcal/kg/hr for animals No. 1, 3, 4, 5, 6 and 8 with a mean weight of 2.01 kg (Table 10, Chapter VIII).

   Assume E_F = 154 kcal/day

7. The maximum M.E. intake is 131 kcal/kg body weight/day (Chapter VIII). For a 2.05 kg animal the maximum M.E. intake is 268 kcal/day. Assume that the maximum M.E. intake per day is 270 kcal.

APPENDIX B

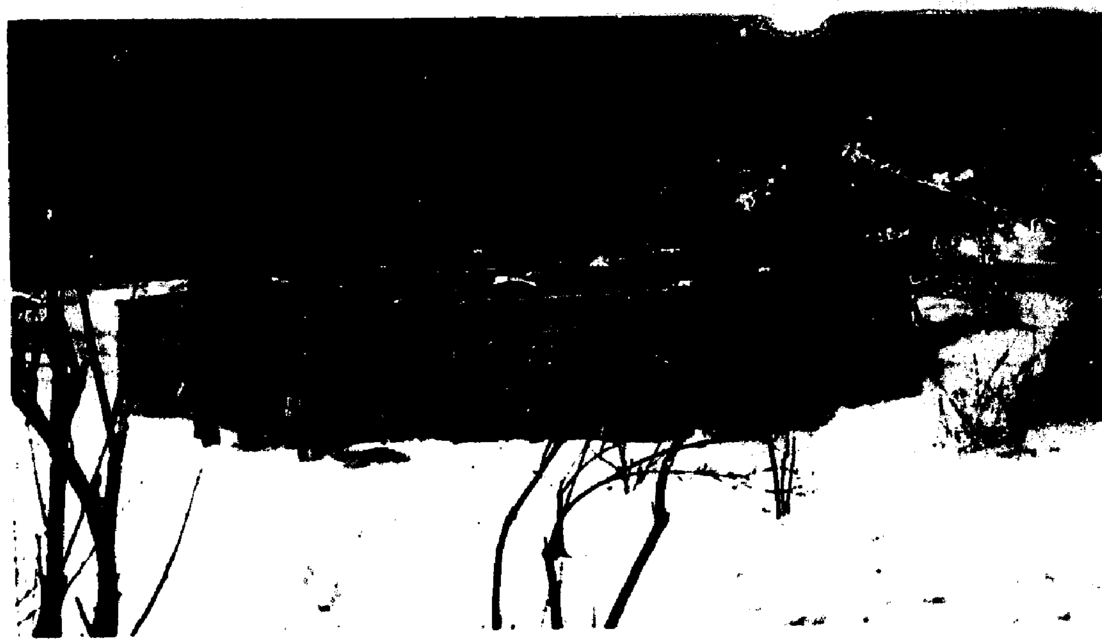
FIGURES

Figure 30. Opossums No. 2 (left) and No. 4, a female and male respectively, provided data on winter energy expenditure, activity and den use.

Figure 31. Metabolism cages (upper left) used in the food balance study.

Figure 32. The complex of eight experimental pens with artificial dens. An anemometer and two Tempscribe recorders are located in the foreground. The electrical wires lead to a recorder in the shed on the right.

Figure 33. An overhead view of experimental pens.



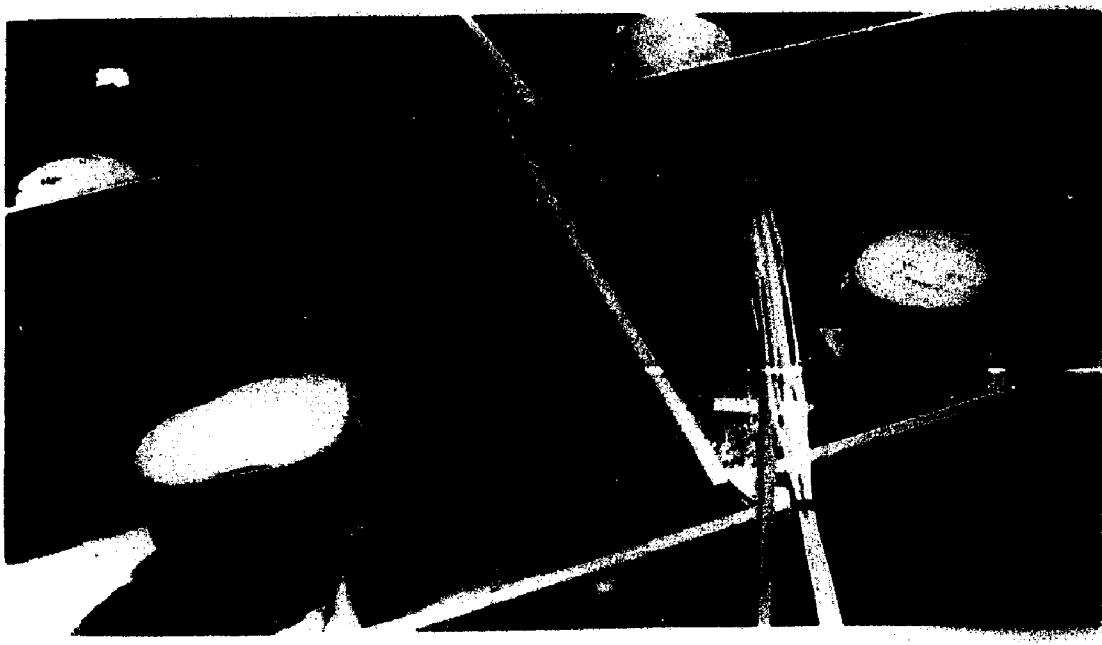


Figure 34. Wooden liners used in the construction of artificial ground dens are in the foreground. The den cavity is located at the apex of the V-shaped tunnel excavation. In the background, the Tempscribe recorder (located above-ground in the final installation) stands on the den cavity liner.

Figure 35. Detail of the den cavity and wooden liners located 1 m below ground surface, at the junctio[n] of the two tunnels. The temperature probe projected into the den cavity through the wooden liner on the left. Straw was used to line the bottom of the cavity.

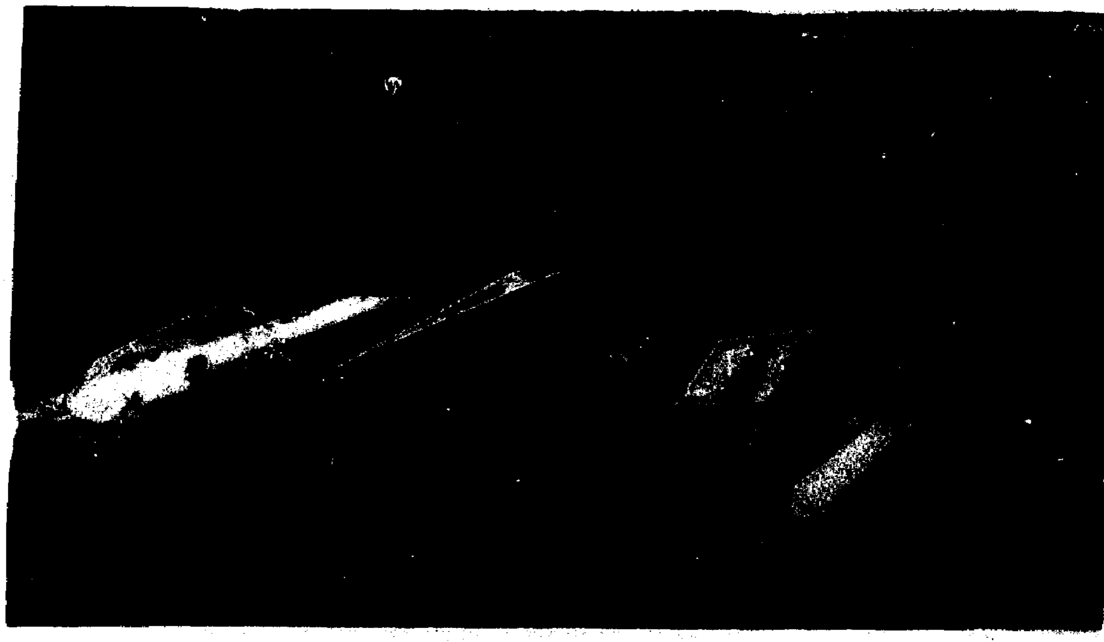
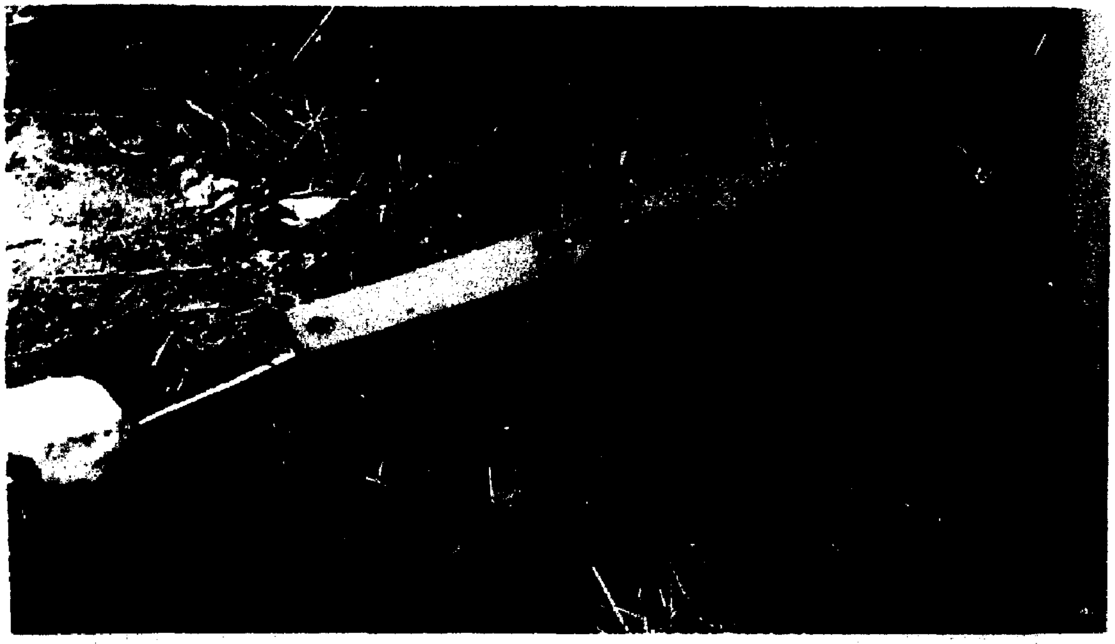


Figure 36. A tunnel entrance with the overhead electrical switch.

Figure 37. An artificial tree den constructed from a sectio of a hollow log. Note the tripping wire of the electrical switch.



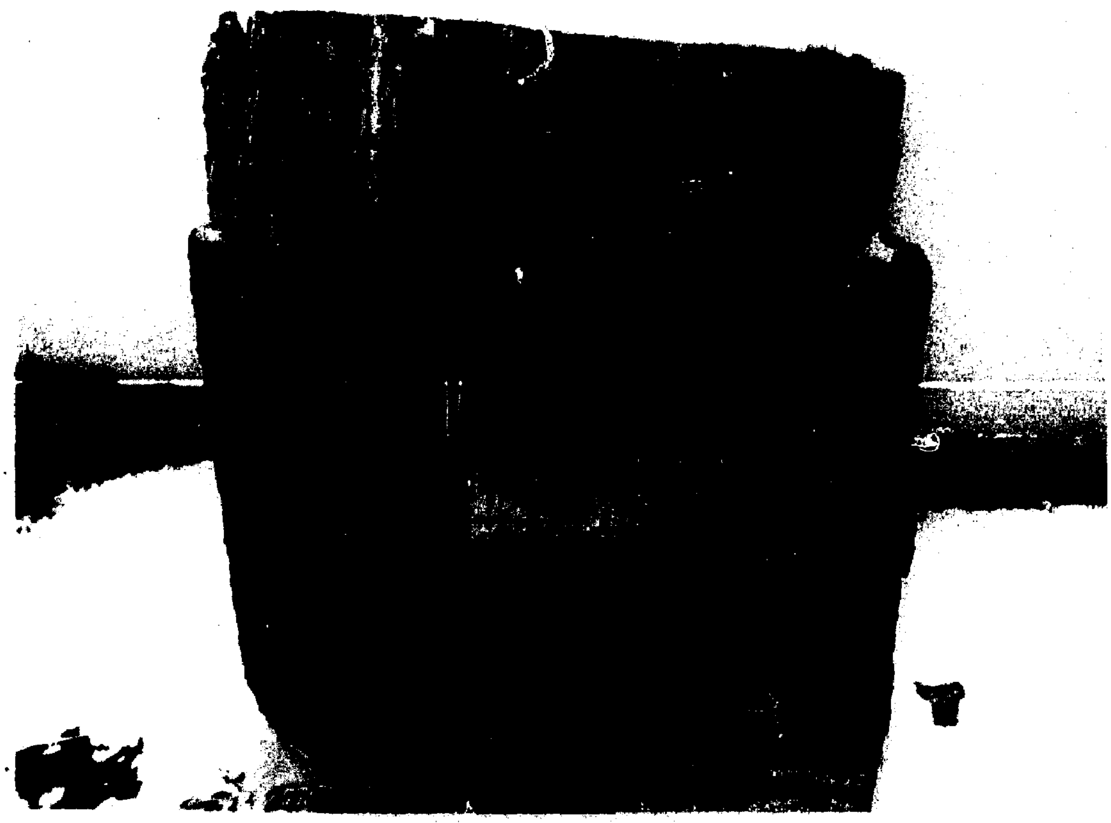


Figure 38. Cover types common on area I. The open plantation in the foreground consists of red pine (*Pinus resinosa*) and white spruce (*Picea glauca*). In the background are black locusts (*Robinia pseudoacacia*) and honeysuckle (*Lonicera tartarica*) near the location of Den No. 5.

Figure 39. A stand of sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), white oak (*Quercus alb*[illegible] and black oak (*Quercus velvutina*) where Den No. 6 was located on Area I.

Figure 40a. Lowland woods with American elm (*Ulmus americana*), rock elm (*Ulmus thomasi*), basswood (*Tilia glabra*), swamp white oak (*Quercus bicolor*), red maple (*Acer rubrum*), tamarack (*Larix laricina*) and red-osier dogwood (*Cornus stolonifera*) bordering a stream. The two sets of tracks on the stream ice (pictured in detail below) are of an opossum and a raccoon.

Figure 40b. Detail of the opossum (above) and raccoon trails on the stream ice pictured in the figure above.

Figure 41. The only tree den observed to be used by an opossum in winter was in the base of this black oak.

Figure 42. Opossum and skunk tracks at the entrance of Den No. 7, the most heavily used ground den.

Figure 43. Copy of Nestell's letter about an opossum carrying leaves.

Flint, Mich.
2-9-69

Dept. of Natural Resources
Game Division

Dear Sirs,

Last Friday morning at about 2 a.m., I saw an opossum do some things I have never seen or heard of before.

I live in Grand Blanc Township, and have a smoke tree, mulched with leaves, just twelve feet from an enclosed porch. I saw the animal under the tree, apparently putting leaves in its pouch. I had a bright flashlight on it, which it ignored. It would grab some leaves (two or three) in its mouth and jam them down between its front legs. Then it would kind of squat with its hind legs and drag itself forward a few inches. By that time it had circled the tree and was going away from me. Now, here is the pay-off! It had its tail wrapped around a bunch of leaves, holding them close to its body and carrying them that way. I could see two turns of the tail around the leaves.

I watched for perhaps three minutes at a distance of twelve feet. When it left, it was carrying them that way. I could see two turns of the tail around the leaves.

I watched for perhaps three minutes at a distance of twelve feet. When it left, it was carrying the leaves and not dropping as many as I would have. Is this the regular behavior of an opossum? I am curious and hope you can give me the dope on its actions.

Sincerely,

M. E. Nestell
2227 Chapin St.
Flint, Mich. 48507